PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol 8(sp1): 25–32
https://doi.org/10.14719/pst.1543

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REVIEW ARTICLE

Stress mitigation strategies of plant growth-promoting rhizobacteria: Plant growth-promoting rhizobacteria mechanisms

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ARTICLE HISTORY
Received: 12 October 2021
Accepted: 25 December 2021
Available online
Version 1.0: 12 February 2022

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, etc. See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

CITE THIS ARTICLE

Sharma V, Singh A, Sharma D, Sharma A, Phogat S, Chakraborty N, Chatterjee S, Purty R S. Stress mitigation strategies of plant growth-promoting rhizobacteria: Plant growth-promoting rhizobacteria mechanisms . Plant Science Today 2022;8(sp1):25-32. https://doi.org/10.14719/pst.1543

Abstract

One of the major challenges that the world is facing currently is the inadequate amount of food production with high nutrient content in accordance with the increase in population size. Moreover, availability of cultivable area with fertile soil is reducing day by day owing to ever increasing population. Further, water scarcity and expensive agricultural equipment have led to the use of agrochemicals and untreated water. Excessive use of chemical fertilizers to increase crop yield have resulted in deleterious effects on the environment, health and economy, which can be overcome to a great extent by employing biological fertilizers. There are various microbes that grows in the rhizospheric region of plants known as plant growth-promoting rhizobacteria (PGPR). PGPR act by direct and indirect modes to stimulate plant growth and improve stress reduction in plants. PGPRs are used for potential agriculture practices having a wide range of benefits like increase in nutrients content, healthy growth of crops, production of phytohormones, prevention from heavy metal stress conditions and increase in crop yield. This review reports recent studies in crop improvement strategies using PGPR and describes the mechanisms involved. The potential mechanisms of PGPR and its allies pave the way for sustainable development towards agriculture and commercialization of potential bacteria.

Keywords

Abiotic stress, Agriculture, Phytohormones, Plant growth-promoting rhizobacteria, Siderophore

Introduction

Around 5.2 billion hectare of cultivable land are affected by various abiotic stresses such as drought, salinity and extreme temperature stresses (1, 2). Due to different stresses, plants undergo different physiological and morphological changes (3). In some plants, leaf growth is reduced due to high salinity and loss of water absorption capacity (4). Several studies on toxicity of heavy metals such as lead, cadmium, cobalt, arsenic were also studied (5, 6). These heavy metals are naturally occurring elements that have higher density than water. Plant needs certain metals in a limited amount for their growth, and some of the metal that is present in the soil mixes up with the soil particles and the remaining metal particles accumulate in the soil in high amounts that increases the toxicity in the soil. Metal toxicity also affects the function, activities and physiological state of plants.

Plant growth promoting rhizobacteria (PGPR) are the free-living soil bacteria and due to root exudates, they are capable of colonizing the rhizospheric region of plants. There are two major classes of rhizobacteria, intracellular PGPR (iPGPR) and extracellular PGPR (ePGPR) (7). In general, extracellular plant growth promoting bacteria exist in/on the rhizospheric region, rhizoplane and intracellular spaces in the root cortex while the intracellular plant growth promoting bacteria exists inside root cells generally called as nodular structures (8).

Many research have shown several benefits of PGPRs in improving plant growth and development (9). Under extreme environmental conditions, rhizospheric bacteria have been found to be beneficial for developing abiotic stress tolerance and crop improvement (10). Inoculation of PGPR strains to plants that are under high salinity alleviates the growth of the plant by tolerating such stresses. Strains like *Pseudomonas putida* improves drought stress tolerance in chickpea (*Cicer arietinum*), similarly other strains like *Bacillus thuringiensis* in soyabean results in modification in the root structure under water deficit conditions (11, 12). For eradication of heavy metals, metal resistant rhizobacteria can serve as an effective method for sequestering of heavy metal. Strains such as *Kluyvera ascorbata* showed high levels of heavy metal resistance and better seedlings growth under heavy metal stress. Other strains, such as *P. putida* and *Azospirillum* are characterized by the development of metal toxicity (8). PGPRs improve and increase the uptake of nutrients by plants from the soil (13, 14). Neutralizing plant stresses (both biotic and abiotic), an important effect of PGPR reduces or prevents the harmful effects of phyto-pathogenic organisms. PGPRs play important role in enhancing crop productivity through mechanism of phytostimulator, biofertilizer, biopesticides and rhizoremediation (13, 15, 16).

PGPRs promote the growth of plant by enhancing the uptake of nutrient and improving the growth expansion and inducing the level of hormones in plants. They act either directly or indirectly to stimulate plant growth and enhance stress tolerance. Direct modes of action include nitrogen fixation, and production of phytohormones, thereby neutralizing various abiotic stresses. Indirect mechanisms prevent or suppress the negative effects on the plant that increase the natural resistance of the host. These mechanisms also help plants to thrive under environmental stresses or disease-based stress (17).

Direct mechanism of PGPRs

The direct mechanism facilitates the uptake of nutrients and/or increases the availability of nutrients through nitrogen fixation, production of phytohormones, and mineralization of soluble nutrients. The uptake of minerals increases due to the influx of ions in the root system. Studies over the last half century have found variants of PGPR, which have been used extensively so far, including the genera of *Klebsiella, Pseudomonas, Azotobacter, Enterobacter, Variovorax, Bacillus, Azospirillum* (18). These bacterial communities possess valuable and essential nutrient properties such as nitrogen and phosphorus for the plant growth. Using different crops and species of rhizobacteria various studies and formulations have been developed around the world (19).

Mechanism of Nitrogen fixation

Biological nitrogen fixation is accomplished through a non -symbiotic or symbiotic relationship between a host, pathogen and a plant. PGPR immobilizes atmospheric nitrogen in the soil and has a symbiotic relationship. Several studies have reported that inoculation with rhizosphere bacteria had shown to improve the soil quality and enhances nodule formation (20, 21). These nitrogen-fixing PGPR inoculants can increase the yield of cereal crops, maintain the level of nitrogen in cropland and improve stress tolerance and aid in disease management. The commercial inoculants *Azospirillum* produced are very effective in increasing the yield of crops worldwide (22). In legume rhizobacteria, the release of ammonia is part of their nitrogen fixation process. There are some C3 and C4 plants, such as wheat, maize, rice, cotton, sugar cane and Jatropha which are involved in interaction with some PGPR and contribute to the growth of grain yield and vegetative phase (23).

Mechanism of phosphate-solubilizing bacteria

Phosphate solubilizing bacteria (PSB) are ubiquitous and belong to the PGPR group and their properties allow rhizobacteria to dissolve phosphate in the soil (15, 24). There are various mechanisms used by PSB to convert insoluble phosphates to soluble form. The bacterial mechanism consists of dissolving organic phosphates in the soil by the action of acids such as gluconic acid that is being synthesized by soil bacteria (25, 26). The mineralization of phosphates is another important mechanism that is carried out by soil bacteria which synthesize extracellular phosphatase enzymes, such as phytases and nucleases to catalyze the hydrolysis of phosphoric esters, followed by release of the phosphate group (27). Solubilization and mineralization both occur in the same bacterial strain. Several bacteria which employ this mechanism to genera *Azospirillum, Serratia, Azotobacter, Rhizobium, Burkholderia* and *Pseudomonas* (28). The microorganisms involved in these three domains, include eukaryotes, bacteria and archaea. The important mechanisms for solubilizing inorganic phosphate are acidification, chelation, and enzymatic action. By secreting acidic and alkaline phosphatases, or by generating organic acids, they induce the mineralization of organic phosphates. Bacterial genera such as *Burkholderia, Rhizobium, Bacillus, Natrinema, Serratia* and *Pseudomonas* have been reported to be potent and effective phosphate solubilizers. The combination of plant growth promoting bacteria with phosphate solubilizers or phosphate solubilizer alone is helpful in improving the uptake of phosphate by crops, thus improving their yield due to environmental and agricultural sustainability (29).

Mechanism of Phytohormone production

Phytohormones are low molecular weight plant growth regulators that are produced at one site and are then transferred to different sites where they play an important role in promoting the growth and development of plants (30, 31). Many PGPRs induce the production of phytohormones and are involved in plant-microbe interaction and are responsible for root growth and architecture (9, 32). In rhizobacteria, Indole-3-acetic acid (IAA) is synthesized from tryptophan, involved in root growth and development (33). Some rhizobacterial strains produce gibberellins that initiate plant shoot growth enhancement (34). Similarly, there are other strains e.g. *Pseudomonas stutzerI*, *Stenotrophomonas maltophilia* and *P. putida* produce the plant hormone cytokinins, which lead to the production of root exudates, thereby increasing the availability of PGPR to plants (30). Other PGPR produces hydrogen cyanide, that acts as biocontrol agent and has potential to inhibit the deleterious pathogen for e.g. *Pseudomonas* (35).

Phytohormone: Auxin

Auxin is one of the most important type of plant growth enhancer in the form of Indole-3-acetic acid (IAA) and Indole-3-butyric acid (IBA) and their precursors. The production of auxin by plants and microorganisms differs due to the biosynthetic pathway followed by them (33, 36). In general, bacterial species have the maximum capacity for auxin synthesis. The activity of auxins to act as growth promoters depends on bacterial and plant species. Some of the rhizosphere bacteria which can synthesize auxins includes *Aeromonas punctata* PNS-1, *Serratia marcescens* 90–166, *Azospirillum brasilense* Sp245, *Pseudomomas putida, Pseudomomas moraviensis, Paenibacillus illinoisensis* IB 1087 and *Pseudomonas extremaustralis* IB-K13-1A. Various studies have shown that IAA acts as a plant growth promoter and mutant such as super root and yucca producing IAA have long hypocotyls, more number of lateral root and root hairs, and also on growth of excised stem and hypocotyls and auxin analogs in intact *Arabidopsis* seedlings (37). The adventitious roots production derived from the stem is the effect of auxin induction (38).

Phytohormone: Gibberellins

Gibberellin is the largest group of plant hormones as over 100 different molecules of gibberellins with varying degrees of biological activity are known (39). Legumes are an important source of nitrogen fixation capable of producing gibberellins due to the presence of rhizobacteria within the nodule. When plants form nodules they require the presence of phytohormones such as auxin, cytokinin and small amounts of gibberellins (40). *Bacillus licheniformis* and *Bacillus pumilus* are species of bacteria known for the production of gibberellins (41). This hormone has the property of translocation from the roots to the aerial part of the plant. The effectiveness of gibberellin is increased in combination with auxin by stimulating the root system, improving nutrient supply in the aerial part. *Acetobacter diazotrophicus, Herbaspirillum seropedicae* and *Bacillus* sp. have been confirmed in gibberellin production (42).

Phytohormone: Cytokinin

Some of the PGPR which synthesize cytokinin includes *Pseudomonas stutzeri*, *Stenotrophomonas maltophilia* and *P. putida*. Cytokinin is involved in the maintenance of plant cell division in culture and in various differentiation processes such as primary root growth, callus formation and shoot formation (43, 44). Totipotency is the distinguishing feature of cytokinin from other plant growth regulators, which helps to maintain totipotent stem cells in their root and shoot meristem. In transgenic plants, endogenous cytokinin overproduction induces diverse phenotypic alterations *in vitro*. The interaction of auxins and cytokinins leads to the control of various essential developmental processes in plants, mainly in the apical dominance and the development of roots and shoots. In the case of *in vitro*, the major regulator of organogenesis is the balance between auxin and cytokinin. In callus culture, a high auxin to cytokinin ratio initiates root formation, while a low ratio results in shoot formation (45, 46).

Phytohormone: Ethylene

Ethylene is a phytohormone that acts as a multifunctional regulator of plant growth. Depending on its time of application, concentration and plant species, it acts as a promoter and inhibitor to plant growth (47). The precursor of ethylene hormone is 1-aminocyclopropane-1-carboxylate (ACC), which is hydrolyzed by the enzyme ACC deaminase, generates ammonia and ketobutyrate. Under stress conditions like flood, and water scarcity, the amount of ethylene is high which tends to inhibit the growth of the plant and especially seedlings (48). ACC deaminase regulates the production of ethylene under stress conditions and promote plant growth by reducing harmful effects on plants (49). Many genera of the PGPRs have ACC deaminase activity which includes *Aneurinibacillus, Arthrobacter, Achromobacter, Bacillus, Brevibacterium, Burkholderia, Citrobacter, Enterobacter, Leclercia, Micrococcus, Ochrobactrum, Parastrephia, Pseudomonas, Ralstonia* and *Serratia.* These PGPRs mitigate the adverse effect of stress manifested on plants by minimizing the ethylene emission to its optimum level and thus confers growth promotion and stress tolerance in stressed plants (50).

Phytohormone: Abscisic acid

Abscisic acid (ABA) plays an important role in many physiological processes in plants. This hormone is necessary for regulation of several events during late seed development and is crucial for the response to environmental stresses such as desiccation, salt and cold. ABA acts like ethylene in stressed conditions and comes under the category of both plant growth promoter and inhibitor depending upon different conditions (51). Some of the species reported to induce ABA production in plants includes *Bacillus megaterium*, *Azospirillum brasilense* Sp 245, *Bacillus licheniformis* Rt4M10. Plant injected with *A. brasilense* Sp 245, *B licheniformis* Rt4M10 resulted increased ABA concentration and higher resistance against stressed condition (52).

Exopolysaccharides production

Exopolysaccharide (EPS) are extracellular carbohydrate polymer that are secreted by rhizobacteria (53). EPS works in two different ways, one by forming a capsule layer which is bound to the cell wall and the other by being released into surrounding cells such as extracellular slime layer. The synthesis of EPS is due to stress response (54). EPS performs various important activities such as plasma substitution and bioremediation, biofilm formation, gelling, antibacterial activity against predators and maintain the main cellular functions, the kinetics of reduction of contaminants, the prevention of desiccation of bacterial cells. EPS producing bacteria are capable to maintain higher soil moisture content and growth of plants even under severely dried sandy soils (55-57).

Mechanism of Siderophore production

Siderophores are low molecular weight compound (400-1500 Dalton) produced by bacteria and plants. Bacterial siderophore has been classified into 5 categories namely hydroxamates, catecholates, peptide siderophores, mycobactin and citrate hydroxamates (58). In aerobic environments, iron exists in an insoluble form, where it exists in the trivalent state as the oxyhydroxide (59). Iron in this trivalent state is sparingly soluble and therefore it is not available to microorganisms and plants, which need iron in the form of Fe^{+2}. In response to this, microorganisms use a pathway to take up this essential nutrient. This pathway is involved in the production of accessory low molecular weight molecules with an abnormally excessive empathy for Fe^{+3}. The bacteria that produce siderophores act as biocontrol agents (60). These siderophores helps the plants to take up Fe^{+2}, where Fe^{+3} ion and a siderophore forms a complex in the membrane in which Fe^{+3} is reduced to Fe^{+2}, which is released into the cell by the siderophore (17). There are over 500 siderophores known to date, which demonstrate the advantage of bacterial siderophores for plant growth (a) nutrient acquiring ability of sunflower plant under stress using *Bacillus sporothermodurans* (61), (b) reduction of heavy metal stress using siderophore producing *Mesorhizobium* sp. (62), during this reduction process siderophores can be destroyed or recycled. The siderophores release iron by reduction via ferric reductase, or by chemical modification or breakdown of the ferric siderophores complex by acetylation and esterase. They also prevent the phytopathogens from acquiring the appropriate amount of iron, thereby limiting their ability to proliferate.

Indirect mechanism of PGPRs

PGPRs exhibits indirect biocontrol mechanism to suppress disease caused by pathogens. The indirect mechanism includes the stimulation of plant growth and the induction of acquired systemic resistance. Biotic stress is often faced by the cultivated and native plants when they are infected by many pathogens like viroids, fungi, bacteria, viruses, nematodes, protists and insects, resulting in significant loss in the crop productivity (63). The fungi cause the maximum biotic stress to the plant. PGPR, such as *Bacillus subtilis*, *Bacillus amyloliquefaciens* strain HYD-B17, *Paenibacillus polymyxa* strains B2, B3, B4, *B. licheniformis* strain HYTAP-B18 and *B. thuringiensis* strains help in combating biotic stress conditions. Studies have shown that plants inoculated with such strains increase root structure under biological stress conditions (64).

Hydrogen cyanide production

Hydrogen cyanide (HCN) production is induced indirectly by the production of siderophores, lytic enzymes etc. Hydrogen cyanide functions as biocontrol agents, chelation of metals and it indirectly increases the availability of phosphate (65). Bacteria, fungi, algae and plants produce HCN, which is toxic to plants by colonizing the roots of plants and reduces their growth. When the host plant was introduced to a cyanide-producing strain, this host-specific rhizobacteria was used as a biological weed control agent, with no negative effects on the host plant (66). Another advantage is the secretion of a secondary metabolite that functions in weed control as a biological control. HCN can also induce cell death by inhibiting the energy supply of cell and electron transport chains. *Bacillus* and *Pseudomonas* species are species with an HCN production mechanism (66). The production and synthesis of HCN by PGPR are independent of their genus and their impact suggested their possibility to use as biological fertilizers or biocontrol to enhance crop production.

Induced systemic resistance

Induced systemic resistance (ISR) is an extensive phenomenon that has been studied and has potential to protect plants against any stresses and pathogens (67). The improved defensive capacity is a physiological state that responds to stimuli in the environment. In the case of local infection, ISR triggers cascades of signaling pathways, activation of certain genes, resulting in protection of plants (67, 68). Strains like, *Serratia marcescens* are helpful in plant growth and in inducing systemic resistance mechanisms to aid plant growth and to increase salt tolerance of wheat (69). Induced systemic resistance (ISR) is an indirect method of PGPR which is beneficial to plants by competing for production of parasitism, nutrient, metabolites and antibiotics. Systemic acquired resistance (SAR) is equivalent to ISR. This is because of induced systemic resistance, a resistance developed by PGPR and SAR is the resistance caused by the pathogen infection in plants.

PGPR- the benefitting technology, future aspects and scopes

Bacteria have a variety of benefits that could be beneficial in commercial agriculture (70). Rhizobacteria and its beneficial strains have improved productivity and agricultural yields by virtue of its mechanism and mode of action (Table 1). The rhizobacteria not only acts as a biocontrol agent, but also in sustained maintenance, protecting plants and most importantly elicit positive effect on field conditions that were affected by stress conditions (8, 71).

Strategies have been developed using a PGPR preparation, so that the bacteria of interest benefit from colonization more than others. Under field conditions, inoculation improves product quality, stability and compatibility. Mechanisms of binding to PGPR as well as to plant-associated biofilm have been established for plant parts such as leaves, roots and seeds. This method has one advantage i.e. higher resistance to antibiotics, which improves the chances of crop survival under stressful soil conditions e.g. *Pseudomonas*, *Azotobacter* (84, 85). To promote microbial growth, Biochar (transport material for microbial inoculant) has the ability to increase crop yield, organic matter content, improving soil fertility by affecting the survival of microorganisms in the soil and maintaining nutri-

Table 1. The uses of plant growth promoting rhizobacteria in improving the plant growth

Plant/Host	PGPR	Uses	References
Vinca rosea	*Bacillus megat Arium*	Stress elevation Ni phytoextraction	(72)
Prosopis juliflora	*Bacillus staphylococcus*	Improves efficiency of phytoremediation	(73)
Oryza sativa	*Agrobactum fabrum*	Increased phytoremediation, decreased toxicity in soil	(74)
Indian mustard	*Kluyvera ascorbata*	Decreased plant growth inhibition by heavy leaves	(75)
Glycine max	*Bradyrhizobium japonicum*	Excess in plant biomass, growth in high arsenic concentration	(76)
Arabidopsis thaliana	*Pseudomonas putida*	Improves utilization of secondary metabolites	(77)
Azospirillum lipoferum	*Triticum aestivum*	Promote development of root system	(78)
Azospirillum spp.	*Zea mays*	Increased growth under drought conditions	(79)
Bradyrhizobium japonicum	*Zea mays*	Synthesize IAA adequate to promote morphological changes and promote growth	(80)
Enterobacter sp.	*Oryza sativa*	Promote seedling growth under salt stress	(81)
Bacillus subtilis	*Brassica juncea*	Facilitate nickel accumulation	(82)
Pseudomonas fluorescens	*Phaseolus vulgaris*	Prevent halo blight	(83)

ents thereby preventing plants from resisting fungal predators (86, 87).

The development of these methods along with the mode of action and/or mechanism of PGPR not only improves the growth of plants, but also increases the yield in the field with less use of fertilizer. For strains showing positive response are potential agents and bio stimulants (88, 89). The relationship between plants and pathogens has been studied for over years. PGPRs that promote growth of plants are very promising in combating negative responses of crops under stress conditions. Thus, it is clear that PGPR has great potential in sustainable crop management and mainly focuses on stimulating plant growth especially under adverse conditions (90).

Acknowledgements

All authors acknowledge the GGS Indraprastha University, New Delhi for providing financial (FRGS Grant No. GGSIPU/DRC/FRGS/2021/594/20).and infrastructure support. RSP also like to thanks SERB, DST India for financial support (Grant No. EEQ/2016/000166).

Authors contributions

NC, SC and RSP designed the study. VS, AS, DS, AS and SP wrote the initial manuscript. All authors read the edited manuscript for critical content and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare .

Ethical issues: None.

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