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Review Article

Plant Growth Promoting Rhizobacteria (PGPR) and their various mechanisms for plant growth enhancement in stressful conditions: a review

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ABSTRACT

The population has been rising in a rapid state and so is the demand of basic necessities like food requirements. Today agriculture demands increase in yield with a substantial decrease in chemical fertilizer and pesticides that are responsible for huge environmental degradation. Today a huge part of yield has been lost due to various stresses plant are subjected too. It could be broadly divided into biotic and abiotic stress. Meanwhile, plant growth promoting rhizobacteria has promised us a substantial agriculture development platform. These are generally a group of microorganism that is found either in the plane of the rhizosphere or above root impacting some positive benefits to plants. These stresses include but in no sense limited to ion toxicity, pathogen susceptibility, physiological disorder, salinity, temperature, flooding, pH etc. In response to the above-mentioned stresses plant with PGPR exhibits various sorts of response to handle these unfavorable conditions. They could be further divided into direct and indirect mechanics. PGPR has shown both synergistic as well as antagonist interaction with microorganism inhabiting in near surrounding to boost plant favorably. This review has tried to undertake all possible mechanism of PGPR along with reported studies for various possibilities through which sustainable agriculture development could take place. This review has tried to understand the mechanism to take PGPR at a commercial level under bio-fertilizer.

Keywords: Microbes; Antibiotic production; Plant growth promoting rhizobacteria; Siderophore production; Phosphate solubilization; IAA.

1. INTRODUCTION

There has been the significant increase in the population of humans on Earth, particularly in the post-industrial era. With increased population, there has been the surge in basic necessity and demands. Resources are depleting at a very rapid state. It's expected to reach the mark of 10 billion in the next 5 decades. Degrading environment, rising population, increasing demand, exhausting resources, demands some significant change and contribution in the field of agriculture to feed people. A technology that could lead towards sustainable development at the same time increasing the yield [1, 2]. The situation turned to worse in certain circumstances with a fatal blow to the amount of crop production, due to the presence of various stresses that could be either biotic or abiotic. Abiotic stresses that are affecting crop are more likely to be drought, soil pH, soil salinization, temperature, soil sodification etc., are known for their soil degrading capability. Drought in most of the cases likely to end up as the cause behind degradation and desertification of soil. Soil salinization in itself is estimated to degrade around millions of hectares of land in Europe. Over around 13% that makes up to 850 million hectare of land is degraded itself in Asia and Pacific region due to drought, soil salinization etc. While near about 104 million has been degraded in pacific sub-region due to clearance of massive amount of land for further development processes [1, 3].

While various living organism including but not limited to fungi, viruses, bacteria, and the parasite are known to cause havoc and lead to various plant diseases and growth compromised state. Fungi in particular compromises about two by third of total disease that affects plant globally. It ultimately is responsible for the reduction in the yield of a plant, which has been estimated around to be 30% globally [2]. While few of probable solution to tackle these problems include but not limited to it are an efficient way of land management, increase in use of chemicals in terms of fertilizer, use of herbicides or pesticides, increase in the transgenic crop, or alternatives like PGPR plant growth promoting rhizobacteria. Many of the above-mentioned solutions are not so beneficial in long-term, because it ultimately leads to various kind of pollution. Fertiliser and pesticides are the common examples of it.

One such case is of nitrogen, around 74% of nitrogen emission in the form of N_2O in the U.S. has been due to nitrogenous fertilizer. It ultimately leads to global warming and the rise in greenhouse gases. Further, it leads to the reduction in nitrogen fixation carried out by microbes, since nitrogen is easily available leading to a reduction in the number of symbiotic association. Moreover, it also results in theses free existing microbes to utilize the provided ammonium and to convert it into nitrate and finally into N_2O which leaches out to carry water pollution [4-6]. Sustainable development in agriculture includes but not limited to disease-resistant plant, drought tolerance, salt tolerance, better quality of yield, tolerance to heavy metal pollution. Along with developing the procedure has to be equally eco-friendly, cheaper and could be carried out in long run. One such method involves the utilization of microorganism like fungi, bacteria, algae etc. They help in increasing water efficiency, suppress pathogenic activities and also lead to uptake of nutrition [7-9].

The nutrient-rich area in soil that is in direct influence of root secretion system is called as rhizosphere. This primarily consists of amino acids, carbohydrates etc. and serves as the source of energy for all the microbes in symbiotic association. The bacteria species present in this zone are known as rhizobacteria. On the basis of their result of the interaction, microorganism has been divided into beneficial, neutral, and deleterious [10-13].

PGPR is one such promising microorganism in this case that's come under beneficial section. While PGPR includes various species like *Arthrobacter, Variovorax, Azosprillum, Alcaligenes, Enterobacter, Bradyrhizobium, Burkholderia, Serratia, Azobacter, Klebsiella, Mesorhizobium, Rhodococcus, Streptomyces, Flavobacterium, Bacillus, and Pseudomonas* etc. [14-17]. However, PGPR has been highly constrained to the certain area for their application. It is due to inconsistent attributes of PGPR, while its effects depend over various factors like its survival in soil system, ability to interact with already present microflora of that place, the factor associated with the environment, and its compatibility with the crop that has been under consideration with its varied number of mechanism to act. [18-21]. PGPR is the term coined by Kloepper around 1970s and in due duration, it is also come to know as (NPR) nodule promoting rhizobacteria and (PHPR) plant health promoting rhizobacteria found in the rhizosphere [22, 23].

PGPR regulate growth through various indirect and direct mechanism. It may include the addition of compounds related to microbe metabolism [24, 25]. They could also act and proved to be beneficial by the production of various inhibitor compounds, bacteriocins, lytic enzymes, siderophores, phosphate solubilization, and could also play a role in the synthesis of phytohormones [26-28]. This review will explore the various beneficial and harmful aspect of PGPR. It will also dwell with the various way a PGPR could roll on its beneficial aspect on the plant.

2. PLANT GROWTH UNDER STRESS CONDITION

Growth and sustainable development and production of the plant is sum total of various rate limiting stresses that are part of the soil environment. The number of biotic and abiotic stresses acts during growth and development. The former include stresses in forms of pathogens and different types of the pest like nematodes, fungi, viruses, bacteria, insects etc. While later includes drought, salinity, heavy metals, flooding, nutrient deficiency, gases etc. As an effect of these yield reduction, hormonal imbalance, nutritional imbalance, and disorders like epinasty, senescence, abscission and disease susceptibility [29-31]. On the basis of different scenarios there has been the particular negative effect which has been observed. For example, stress condition like waterlogging, drought and salinity have led to the elevation in the level of ethylene [32]. It is thought to cause inhibition of various plant processes by reducing root growth [33]. While in other stress conditions ion toxicity could be observed on the plant with injurious effect over its growth and development. It occurs due to excessive accumulation of Na and Cl ions [34]. The drought-like condition is known for their ability to inhibit photosynthesis and change in the amount of chlorophyll and distortion in photosynthetic apparatus [35]. At the same time other scenarios like heavy metal accumulation in soil, lack of nutrient, attack of various pathogens etc. could make the plant more susceptible towards disease, metal toxicity, hormonal imbalance etc. [33, 36].

Saline conditions have been further found to be an inhibitor of nodulation production or early senescence of it and reduction in fixation of nitrogen [37]. 26 mM concentration of NaCl has found to reduce nodulation by 50% and its weight [38]. While the lower level of salinity has to seen to lead to a situation of reduction in nodule formation in *Vigna radiate* [39, 40]. In yet another work it has been reported that salinity could result into reduction in the active nodule, water content, nitrogen content and chlorophyll content of *Medicago sativa* [41]. Rhizobium is known for their tolerance towards salinity, yet a high degree of variability could be seen. Salinity is thought to induce effects over rhizobia activity further on to the nodules growth and development and ultimately to the nitrogen fixation by nodules [42]. It too reduces the nitrogenase enzyme activity in microbes. Around 90 mM of NaCl carries complete inhibition of nitrogen fixation [43].

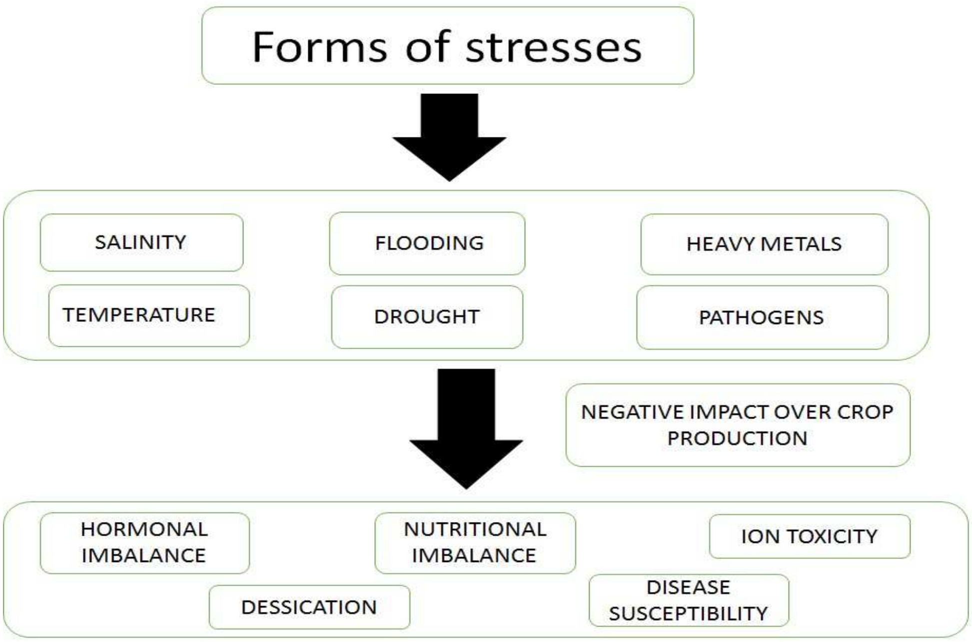

Figure 1. Forms of stresses in plants.

Many people have worked on the variety of stresses plant could be subjected to and its probable effect on growth and development. Over the period of time plant has developed various defense mechanism to fight these stresses [44]. There had been various human-made development in order to counter the stresses like in case of excess ethylene which could be dealt with the application of various inhibitor as cobalt ion (Co^{2+}), amino ethoxy vinyl glycine or it could be the silver ion. But they too have a detrimental effect on soil health, net cash return, environmental and human health. Moreover, they seemed to be helpless in case of ion toxicity or root desiccation [45, 46].

A plant has adopted the variety of mechanism to deal with stresses like the production of various reactive oxygen species that includes the formation of either hydrogen peroxide, hydroxyl radical or superoxide that ultimately enhances plant growth. ROS is supposed to act by cellular damage or lipid and proteins oxidation, bleaching of chlorophyll, and could be a distortion of nucleic acid could be the reason for cell death [47-49]. Further production of various enzymes by the plant in order to survive in stress condition has to been reported. Antioxidant enzymes such as ascorbate peroxidase, catalase, superoxide dismutase, and glutathione reductase are few to be named. When sensitive and susceptible species are compared to tolerant plant species it has been often found that the later possess larger proportion of antioxidant enzyme [50-52].

There are various non-enzymatic anti-oxidant that has been reported to mitigate the stress like condition in plants. It could constitute of various cellular redox buffer, secondary metabolite including but not limited to flavonoids, carotenoids, ascorbate, tocopherols, glutathione, etc. [53-55]. In the saline condition it has been observed that along with various other imbalances in normal processes there has been a reduction in the amount of water uptake. In such a scenario, the plant is found to accommodate various compatible salts like glycine betaine, proline, polyols, trehalose, and many other solutes that are organic in nature. This accumulation helps in managing the lethality like condition that could emerge as a result of osmotic regulation in case of the stress-induced condition. It acts by limiting the amount of water that leaves plant and dilution of further accumulated salts in roots take place [56-58]. They further have a role in the stability of various functional unit and maintaining osmotic potential.

Production of phytoalexins that are antimicrobial in nature, hypersensitive reaction, generation of defense barrier in the form of material like suberin, lignin etc. as well as hydrolytic enzymes are few other plants methodology to mitigate drought like scenario [59]. Accumulation of various metabolite of secondary nature and defense protein synthesis are few of other known defense mechanism of plants [60, 61].

3. PLANT GROWTH PROMOTING RHIZOBACTERIA

These are the group of bacteria that could be seen in the rhizosphere and are known as the promoter of plant growth. It colonizes the part of root and soil environment called rhizosphere. Rhizosphere shows the maximal activity of microbes with the confined environment consisting of many essential micro and macronutrient. Root exudates act as the nutrient source and are responsible for the difference in microbial population between surrounding and rhizosphere. Weller and Thomashow in their work have reported that there is approx. 10 to 100 times increase in microbial population owing to the rich nutrient region of the rhizosphere [62-64]. Algae, fungi, protozoa, and bacteria are found to be part of rhizosphere with the predominant allocation of bacteria in it. Their role has been proven and introduced by Kloepper and Scroth. PGPR is not only associated with roots but also counter the effect of phytopathogenic microorganism. Its potential has been explored in case of an active constituent of biofertilizer [65-70].

On the basis of interaction, these PGPR could be separated out in two type's namely symbiotic and free living. The fact behind former one is that they live inside plant parts and has a direct source of interaction regarding exchange of metabolites while later lives outside. Some symbiotic bacteria usually resides in the intercellular spaces present in the plant while others could get themselves into mutualistic interaction as a way to penetrate inside the plant cell. Yet few members could direct plant into the formation of some specialized structure. Rhizobia, one of the best sort, an example of the mutualistic association of bacteria and plant. It fixes the atmospheric nitrogen into a specialized structure called as root nodule [71-72]. PGPR acts through various indirect, direct and synergistic approach. It has been successfully reported in case of radish, sugar beet, potato and sweet potato [73] but yet the commercial applications require the better understanding of its mechanism and action [74]. The isolates have shown the mixed trait of PGPR as a result [75]. PGPR has shown the magnificent result on plant growth in nutrient deficient as compared to the nutrient-rich region [76].

In the case of *Arabidopsis thaliana* when grown along with some inoculated PGPR, the soil was found to be rich in some volatile compound like acetoin and 2, 3-butanediol [77]. Cotton plant height and seed yield have been increased along with the microbial population in surrounding as a result of the addition of some diazotroph bacterial strain [78]. Apple rooting has been further increased by the addition of double to the triple composition of indole-3-butyric acid along with carbohydrates and bacterial strains [79]. PGPR has been further found to improve the various prospect of chickpea like modulation along with yield and growth when inoculated with compost rich in phosphorous [80].

4. PGPR OVER THE PERIOD OF TIME

Since its introduction, a lot has been done in case of PGPR. A large number of possibilities has been verified and explored with alter parameters responsible for PGPR mechanics. In this due course of time, the number of PGPR has been identified as well as isolated from the various sample and studied. *Azarcus* has been seen along with crop named rice and has been known for nitrogen fixation [81]. In similar fashion, *Azobacte*r has been reported in the case of cucumber for cytokinin synthesis [82]. *Azorhizobium* [83] and *Azospirillum* [84] has been isolated from fields of wheat and sugarcane respectively and have been helpful in nitrogen fixation. *Azotobacter* isolated from a number of crops like maize, barley, wheat, oats etc. has undergone nitrogen fixation [85]. *Bacillus* has been obtained from various crops fields like potato, cucumber, pepper, peanuts maize etc. with wide array of its mechanism like auxin synthesis [86], cytokinin synthesis [87], gibberellin synthesis [88], potassium solubilization [89, 90], induction of plant stress resistance [91, 92], antibiotic production [93] and siderophore production [94]. *Beijerinckia* and *Burkholderia* isolated in associated form from sugarcane [95] and rice [96] crops respectively have been reported to perform nitrogen synthesis.

Chryseobacterium [97] has been associated with tomato crop and act through siderophore production. *Frankia* [98], *Gluconacteobacter* [99], *Herbaspirillum* [100] isolated from *Alnus*, sugarcane, and rice has been helpful in nitrogen fixation. *Paenibacillus* isolated from lodgepole pine and black pepper has been reported for indole acetic acid production [101] and potassium solubilization [102] respectively as a mechanism for enhanced growth and stress management. *Phyllobacterium* has been reported for phosphate solubilization and siderophore production [103]. *Pseudomonas* also has been associated with large varieties of crop and has been proved to beneficial in stress management through the number of mechanism and production it could associate to or could lead to. Some of the reported mechanism are chitinase and glucanase production [104], ACC deaminase synthesis [105], induction of resistance to stress [106], antibiotic production [107, 108].

Rhizobia isolated from legumes and peanuts crop has been reported for nitrogen fixation [109], induction of resistance to various stresses and hydrogen cyanide formation [110]. Rhizobium isolated from pepper, tomato, lettuce, carrot, tomato mung beans etc. has been too reported for some common mechanism like nitrogen fixation [111], indole acetic acid synthesis [112], ACC deaminase production [112] and siderophore production [113].

5. DIRECT AND INDIRECT MECHANISM OF ACTION IN PGPR

A deep understanding of plant growth promoting rhizobacteria is essential for taking PGPR to commercial level and for enhancement of plant productivity and its optimization. PGPR modes of action have been grouped into two subtype's basically direct and indirect mechanism. Indirect is consider to be those that are outside while direct lives in the plant to render their effect on plants metabolism [114]. Indirect mechanics, we usually either sees the integration of various growth factor released by microorganism or microorganism could potentially act as the sink of produced hormone and enhances its adaptive capacity. While indirect mechanism relay over the secondary metabolites and its sensitivity towards signal released from the microorganism. It includes, for example, the induction of resistance to the varied number of pathogen attack or resistance as well as tolerance to varied stress conditions [115-117].

6. DIRECT MECHANISM OF PGPR

6.1. Biological nitrogen fixation

A number of species of bacteria have been found associated with rhizosphere of the plant that adds to the enhancement of plant growth. It includes but not in any way limited to *Erwinia, Azospirillum, Flavobacterium, Bacillus, Alcaligenes, Arthrobacter, Rhizobium, Acinetobacter, Burkholderia, Pseudomonas, Enterobacter, and Serratia* [118, 119]. Selection and proliferation of bacteria as a part of root exudates are done by the plant. The enrichment of bacteria is a function of the availability of different types of organic matter and their specific concentration. The selection also depends on the microorganism ability to utilize organic matter as the source of nutrition. They have an efficient, effective and specific mechanism for uptake of nutrient along with its break down in the form that could probably lead to it as the source of nutrition [119-122]. Bacteria at the very root surface commonly termed as rhizoplane tend to be more efficient than the others. This mutualistic interaction is a result of co-evolution, the inoculated material of microorganism should be verified for their preadaptation. They are further looked up as a substitute for chemical fertilizer, supplements and pesticides at the same time it could prove to be effective for reduction in cost as well [123, 124].

Bacteria along with Archaea are the only group of organism in which the ability to fix nitrogen from the atmosphere has been confined to. They have been well known for their effect over rice and chickpea yield. 180 x 106 metric tons of crop are benefitted with the help of biological nitrogen fixation in a year. Among the total crop benefitted around 80% of it has been accounted to the symbiotic association. Symbiotic nitrogen fixation could be achieved through *Rhizobium* the known obligate symbiotic associated with the leguminous plant, *Frankia* in case of non-leguminous plant and in case of microorganism living freely shows the non-symbiotic nitrogen fixation with associative or the endophytic nature. The microorganisms falling in the later stage are *cyanobacteria*, *Azotobacter*, *Azospirillum*, *Azoarcus*, *Acetobacter diazotrophicus* etc. [125-127].

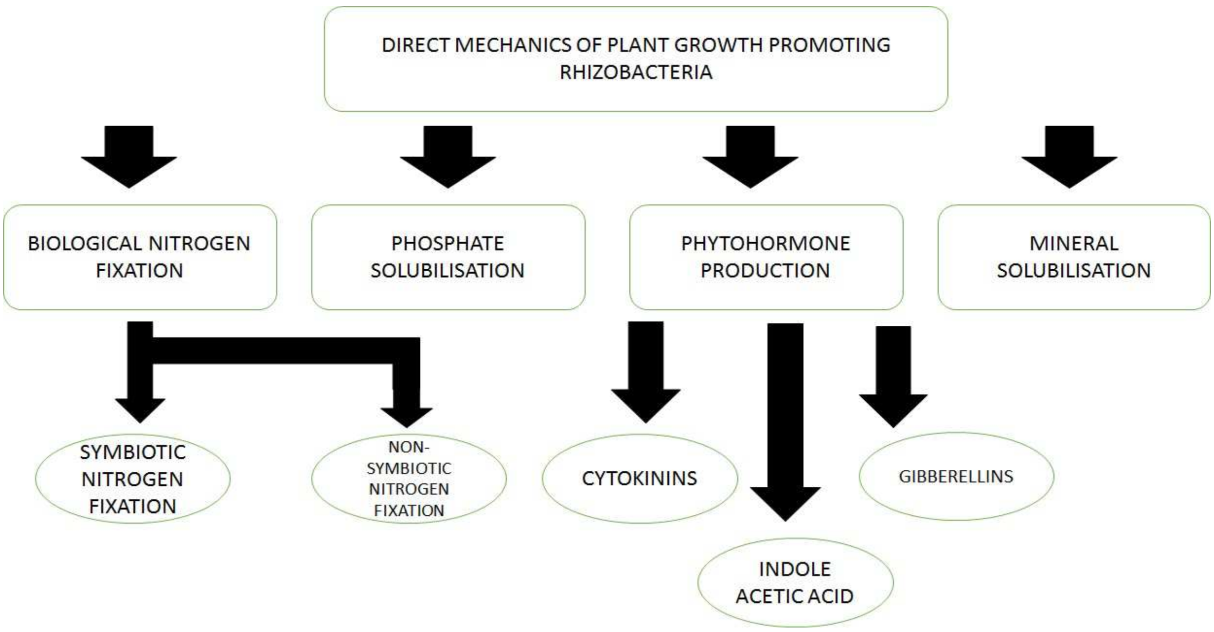

Figure 2. Direct mechanism of plant growth promoting rhizobacteria.

6.2. Symbiotic nitrogen fixation

Rhizobia and *Frankia* have dominant say into symbiotic nitrogen fixation as well as they are highly researched. *Frankia* has been found to be effective in almost eight different families with expansion to about 280 different species [128]. *Alnus* and *Casuarina* species of plant are found to be most benefitted from this association [129-132]. Crop rotation with a leguminous and non-leguminous plant on alternate has led to the conclusion of overproduced rhizosphere after every non-leguminous cycle, with additional benefits for upcoming crop. On the onset of polyphasic taxonomical approach there comes the considerable shift in classification. A total of 36 species has been divided over seven genera consisting of *Rhizobium spp*. [133-135]. In addition to increasing in growth, yield, fixation of nitrogen, they are further reported to regulate deposit of organic and inorganic phosphate in soil and further proved so instrumental in the determination of soil nutrition [136]. Owing to the above-mentioned fact symbiotic nitrogen-fixing bacteria have been further utilized along with phosphate solubilizing bacteria (PSB) that has proved to be beneficial in case of mungbean due to the synergistic effect. The duo has shown around the significant increase of 30-40% on different parameter like shoot weight, yield, plant height, seed content etc. when compared to be inoculated with the individuals one [137]. *Bradyrhizobium* another common organism generally found in symbiotic relationship. It grows well when pentose is being taken as the carbon source [138]. It has been reported that co-inoculation of this bacteria has been proved to be very useful in nitrogen fixation, number of nodulation, dry weight, grain yield, nitrogenase activity, soil nutrient [139-141].

6.3. Non-symbiotic nitrogen fixation

It has an indispensable role to play in agriculture and in nitrogen fixation. The major limitation clouding its effect has been an energy-oriented fixation of nitrogen in a form that plant could easily utilize it. The limitation could be easily dealt with bringing them in closer proximity to roots. Non- symbiotic nitrogen fixation is associated with numbers of bacteria including but not, in any case, limited to *Azoarcus* sp., *Herbaspirillium* sp., *Azotobacter* sp. [142, 143], *Achromobacter, Alcaligenes, Azospirillum, Arthrobacter, Azomonas, Bacillus, Gluconacetobacter diazotrophicus, Beijerinckia, Clostridium, Derxia, Corynebacterium, Enterobacter, Pseudomonas, Klebsiella, Rhodospirillum, Acetobacter, Rhodopseudomonas* and *Xanthobacter* [144]. *Azotobacter paspali* reported by Dobereiner and Pedrosa in the nodule of *Paspalum notatum* is found to be influencing growth and yield [145]. The yield of wheat has been observed to increase by 30% on application of *Azotobacter* [146]. *Azotobacter* and *Azospirillum* are reported to influence crop by increase seedling growth [147-149] along with the seed germination rate [150].

Azospirillum has been on discovery since the 1970s, there had been much of findings in both cereals and non-cereals crop. They are usually considered to be helpful in nitrogen fixation but not always and the reason of the increase in yield is related to fact that it leads to the production of various growth promoter that increases root length subsequently into larger nutrient uptake [151-154]. They are not hosting specific and till now there have been 10 species which has been identified and classified on basis of their molecular and biochemical features: *A. amazonense* [155], *A. lipoferum* and *A. brasilense* [156], *A. halopraeferens* [157], *A. largimobile* [158], A. irakense [159], *A. doebereinerae* [160], *A. melinis* [161], *A. oryzae* [162], and lastly *A. canadensis* [163].

6.4. Phosphate solubilizing bacteria

Phosphorous is the next nutrient on the list which has a great say in plant growth. It acts as limiting nutrient in many of cases studied. Despite its abundance in the soil, it is still one of the major cause in the reduction of plant growth. It has been due to form in which phosphorous is present. About 50% of phosphate present in soil is in insoluble form. They are present in calcareous soil as calcium phosphate. Inorganic phosphate is present in association with different elements like compounds of aluminum or irons. An only soluble form of phosphorous i.e. monobasic and the dibasic form are of any use to plants [164]. Microorganism generally aids the plant by utilizing and converting the different form of the organic phosphorous present in the soil like aluminum phosphate, rock phosphate etc. into the inorganic form that could be easily uptaken by plants and further could be utilized in a way it could be led to development. One of the common mechanism of phosphate solubilization involves secretion of organic acids which is formed as a result of utilization of sugar present in root exudates. These acids that are secreted out acts as a good chelating agent and removes Ca^{2+} cations followed by a release of phosphate from the different compound of phosphate present in soil [165]. In addition to it, they are also well known for their lowered pH medium which is one of its characteristic owned by its various secretion [166, 167].

Phosphate solubilizing microorganism (PSM) has emerged out to be a new alternative in the field of agriculture for sustainable development. It converts the phosphate and leads to easy uptake, is one of its many ways through which it aids a plant [168, 169]. Further study of its ability to colonies rhizosphere, diverse methods of its action, and its utilization as the application could probably lead to a scenario where we can optimize its functioning and could use it for further enhancement of crop [170]. Economically suitable PSM are generally compromised of fungi like *Penicillium* and *Aspergillus* and bacteria like *Pseudomonas, Rhizobium,* and *Bacillus*. Phosphate solubilizing microorganism along with various PGPR has resulted in the lesser requirement of Phosphate along with the enhanced quality of yield, efficient use of fertilizer, lesser pollution and more eco-friendly [171, 172].

PSM constitute about 20-40% of microorganism that could be cultured with a big amount of these are found to be colonized in rhizosphere [173]. Many of them are able to interact with various metal leading to precipitation and hence unable to be available for uptake by the plant. Phytate the so-called hexaphosphate constitute around 80% of the total organic phosphorous present in the soil. The ectorhizospheric stain that usually found on rhizospheric soil or on roots and endosymbiotic strain that colonizes inside the root of Bacilli and *Pseudomonas* are counted amongst the most effective microorganism for phosphate solubilization [174]. While in other work gluconic acid produced by *Burkholderia cepacia, Pseudomonas cepacia, Erwinia herbicola,* and *Pseudomonas fluorescens* has reported being another efficient agent for solubilization of mineral phosphate. *Rhizobium leguminosarum* further lead to solubilization with help of 2-ketogluconic acid. While a mixture of lactic, isobutyric, isovaleric and acetic acid have been too reported to help insolubilization of phosphate [175-178].

6.5. Plant growth regulator and its production

These plant growth associated regulator like GA, auxins, abscisic acid, IAA, ethylene, and cytokines are also known by name of plant exogenous hormones which could be synthetic or natural in nature and similar to hormones produced naturally by the plant. They have an essential role in terms of boosting agriculture production. A microorganism that has the inherent capability to regulate the production of various growth regulator enzyme is known as a plant growth regulator or phytostimulator. These phytohormones are present in the very lesser amount, but influences varieties of dimensions in plant growth like morphological, physiological and biochemical processes of the plant [179, 180].

IAA stands for indole-3-acetic acid is one of the essential auxins which falls under phytohormones. It has an indispensable role in the development of the organ, cellular responses like differentiation, expansion, division, and regulation of genes [181]. A wide number of bacteria has the ability to produce phytohormones like IAA which could be signaling molecule leading to the photostimulating effect on plant along with pathogenesis and induction of colonization [182]. It could further help us to isolate the PGPR strain on the basis of IAA secreting bacteria [183]. Auxin has proved to be a concentration sensitive issue for seed germination. Low concentration has stimulated growth while higher concentration has resulted in its inhibition [184]. The maximum proliferation of crop and surge in yield has been found when stains producing the highest amount of indole acetamide or IAA has been employed along with the crop. The adequate amount of success even in stressed condition has been achieved, when stains with lesser but continuous production of auxin have been inoculated with the crop like wheat, tomato etc. [185-188].

Strains of *Microbacterium, Mycobacterium, Sphingomonas, Rhizobium, Dendrobium moschatum, Kocuria varians*, *P. fluorescens* are few of the many that are known for actively producing phytohormones [186, 187]. *Bacillus* and *Pseudomonas* are others who have been in possession with the phytohormones producing abilities but has not been studied well. The reported studies suggest that bio stimulant species of these genera have been associated with the increase in root length that ultimately leads to increase in the surface area further leading to increase in the uptake of nutrition through the rise in the absorptive area [189]. *Rhizobium* spp. has been first to be identified for phytohormones production and subsequent effect of it has been studied. It has been present in close association with legume hosts or root nodules of *Sesbania sesban* (L) Merr., *Vigna mungo* (L), *Crotalaria* sp., *C. retusa* [189-195]. Along with IAA, there has been the isolation of various other phytohormones like indole lactic acid, indole-3-pyruvic acid, indole-3-butyric acid [196-197], gibberellins [198], and cytokinins [199-200]. Micro-organism associated with plants are reportedly responsible for the production of IAA through L-tryptophan dependent as well as independent pathways with three pathways that are L-tryptophan dependent are known. L-tryptophan that is secreted as part of root exudates is utilized for production. Almost 90% of total production has been estimated to be produced as a result of independent pathway while only 10% has been produced by the known mechanism of tryptophan utilization [201-202].

Ethylene is another in the list which has proven to be potentially active for fruits and leaves maturation, seed germination, leaf senescence, flower wilting, initiation, elongation, and branching of the root, nodule formation and abscission of leaves all at the low concentration. While at higher concentration it has been the cause of defoliation, inhibition of growth in root and stems with senescence at the premature stage. Actually, the plant has been known for producing the precursor of ethylene i.e. 1-aminocyclopropane-1-carboxylate (ACC) in the result of a various form of stresses that it has been subjected to like cold, infection, flooding, drought and even the heavy metal presence [203-206].

7. INDIRECT MECHANICS OF PLANT GROWTH PROMOTING RHIZOBACTERIA

7.1. Production of siderophore

Iron is one of the important element for growth and development of a plant with particularly towards respiration, nitrogen fixation, and photosynthesis. Despite the enormous amount in which it is present at the surface of the earth, yet it is very rarely available for the plant. It is present in the form Fe^{3+} that is insoluble and hence unavailable for plant uptake. The mechanism to get away with this situation includes the release of organic compounds that could simply act as a chelating agent which forms a plant end in a friendly way product which could be easily be uptaken by enzymatic assisted transport system available in plants cell membrane. The second method involves absorbing the organic and Fe^{3+} complex further involving *in vivo* reduction and absorption [207, 223-227].

In order to deal with this problem, PGPR has up taken the production of siderophore as a remediation technique. Siderophore is basically the protein with lower molecular weight usually below 1 kDa with a functional group like catechols, hydroximates, carboxylates etc. that has an affinity to bind an iron molecule, they act as chelating agent for ferric ion in the surrounding. So in Fe deficient moments, they act as a way through which plant meets their demands for iron. Besides ion deficient condition, pH of the surrounding, the presence of trace elements, the supply of another basic thing like carbon, nitrogen too could induce production of siderophore. It has been established in a research that a siderophore producing strains of *Phyllobacterium* have been responsible for growth and development in case of the strawberry crop [208-210].

Bacteria usually belonging to *Pseudomonas*, *Enterobacter*, *Bacillus*, *Rhodococcus* genus are known for the production of siderophore. The concentration of siderophore is basically as low as 10-30 M. The most researched microorganism for the production of siderophore has been *Pseudomonas aeruginosa* and *P. fluorescens* that produces pyroverdine and pyochelin kinds of sideophores.

They have been known for their influencial role in improving irons uptake, inhibiting the growth of pathogens by antibiotic production, and inhibit fungal growth in locality [211-213].

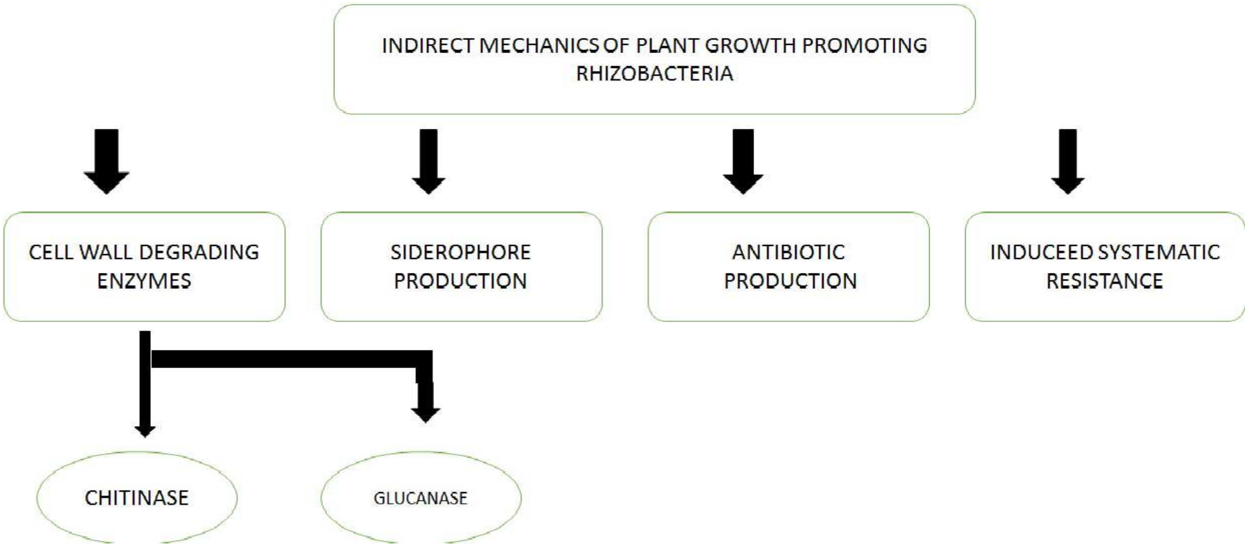

Figure 3. Indirect mechanics of Plant Growth Promoting Rhizobacteria.

Table 1. Types of siderophores and organism responsible for its production [214-219].

Types of siderophores	Organism producing siderophore	Types of siderophores	Organism producing siderophore
Hydroxamate-type of siderophores		**Catecholate type of siderophore**	
Ferrichrome	*Ustilago sphaerogena*	Enterobactin	*Escherichia coli*
Desferrioxamine B	*Streptomyces pilosus* *Streptomyces coelicolor*	Bacillibactin	*Bacillus subtilis* *Bacillus anthracis*
Desferrioxamine E	*Streptomyces coelicolor*	Vibriobactin	*Vibrio cholerae*
Fusarinine C	*Fusarium roseum*		
Ornibactin	*Burkholderia cepacia*		
Mixed ligand and other types of siderophore			
Azotobactin	*Azotobacter vinelandii*	Phytosiderophores or mugineic acids	Poaceae (grasses), wheat and barley
Pyoverdine	*Pseudomonas aeruginosa*	Antibiotic siderophores	Endophytic Actinomycetes
Yersiniabactin	*Yersinia pestis*		

Table 2. Siderophore producing microorganism and there reported effect on crops.

Siderophore producing organism	Application on plants	References
Azotobacter vinelandii MAC 259 *Bacillus cereus* UW 85	Increases the yield of plant	[220]
Bacillus megaterium	Reduces the intensity of disease with growth promotion	[221]
Escherichia coli	Growth of plant with maximum siderophore production	[222]
Pseudomonas putida *Pseudomonas fluorescens*	It helps in increament of yield and production of plant	[219]

7.2. Cell wall degrading enzyme production by PGPR

Production of chitinase as well as glucanase has been long being seen as one of the methods to control the pathogens that have the potential to infect plants. The mechanism undertaken by theses PGPR is the degradation of cell wall affecting the integrity of the structure and hence inflicting inhibiting growth on pathogens. Some of the common enzymes that have been used to degrade cell wall or secreted by PGPR strains to stop the growth of pathogens are cellulose, chitinase, proteases, and β-1,3-glucanase [228, 229]. *Streptomyces* and *Paenibacillus* strains that produce β-1,3-glucanase has shown to have the inhibitory effect on *F. oxysporum*, while the same enzyme produced by *Bacillus cepacia* was reported to show inhibitory effect on the number of soil-borne pathogens *like R. solani, Sclerotium rolfsii, and P. ultimum* [230]. While in case of chitinase it has been chitin that is β-1,4-N-acetyl-glucosamine, and the linear polymer which is being targeted, since it's an important part of fungal cell wall it helps to effectively control pathogens [231, 232]. Organism reported to show above mentioned chitinolytic activities are *B. thuringiensis, B. licheniformis, B. circulans, B. cereus* and *B. subtilis*, while in case of gram negative following organism has been reported *P. fluorescens, Enterobacter agglomerans, Serratia marcescens,* and *Pseudomonas aeruginosa.* When some soil born pathogen like *Fusarium oxysporum and Rhizoctonia solani* has been inoculated with the strain of *Serratia marcescens* B2 exhibiting antifungal and chitinolytic activities lead to several irregularities in pathogen like partial swelling of hyphae, bursting of hyphae at tip and curling of hyphae etc. It has been successfully employed in case of controlling pathogen like *F. oxysporum* and *Sclerotium rolfsii* on beans [233-235].

7.3. Modulation of the stress marker

Plant over the period of time is subjected to the variety of stresses that could be biotic and abiotic. The extensive assortment of environmental stress exposed to plants include but not, in any case, is limited to cold, pH, temperature, drought, alkalinity, pathogen exposure, and salinity. In a report, it has been debated that abiotic stress could lead to the total of 30% of loss in agriculture crop worldwide. In all the kinds of abiotic stresses, salinity holds a particular position in terms of loss of agriculture productivity which is owned to the fact that it leads to a reduction in photosynthesis, nutritional imbalance, reduction in protein synthesis, respiration and oxidative stress with the hypertonic condition. Oxidative stress further results in the formation of various reactive oxygen species like superoxide ions, hydroxyl radicle, singlet oxygen and hydrogen peroxide act as toxic molecules to plant metabolism [236-239].

These reactive oxygen species are reactive in nature with the potential of inflicting damage over nucleic acids, proteins, and lipids. In order to counter the effect, the plant has evolved an effective antioxidant system. Plants store various isoenzymes in its compartment like mitochondria or chloroplast. These isoenzymes have scavenging activity for ROS. It includes ascorbate peroxidase (APX), L-proline, peroxidase (POX), catalase (CAT), superoxide dismutase (SOD), and glutathione reductase (GR). They act as a regulator and keep in check over ROS species. In a report considering *Lycopersicon esculentum* and *B. cereus* AR156 effect over it has resulted into positive conclusion. It is reported that it has an active role in the protection of protein from denaturation by forming folded structures, or in stabilizing cell membrane, could act as the scavenger of radicle ion and also has the potential to act as the energy source as in case of L-proline [240-243].

PGPR strains have further resulted in plants to have induced systemic resistance (ISR) which is the result of various stimulation that happens because of the addition of PGPR secretion. It has resulted into increase in mechanical and physical strength of a plant with some slight modification possible in day to day biochemical and physiochemical reactions of the plant. The result has been obtained in form of peroxidase, chitinase, and lytic enzyme production [242-243].

7.4. Antibiotic production

It has been a while since we are using chemical pesticides in order to boost the productivity of the crop. Despite chemical fertilizer being advantageous to our crop, it has brought substantial distress in long run. Their ability to remain intact for a longer period of time has added to water pollution and soil pollution. Along with that, it has a broad spectrum of action that makes it disastrous even for beneficial microbes. This entire dimension has led to the acceptance of biopesticides that is safe, easy to degrade as well as selective in nature. After the discovery of PGPR strains acting as an inhibitory factor for various pathogenic microorganisms through the production of some metabolites which could lead to suspension of pathogen growth at the minute, the level has open door to new possibilities. Today, microbes antagonistic feature is being looked up as a substitute for the chemical pesticides that have shown the disastrous effect over our environment. This microorganism inhibits phytopathogens through numerous ways like competing for the available nutrient and space, producing bacteriocins, lytic enzymes, and antibiotics [244-247].

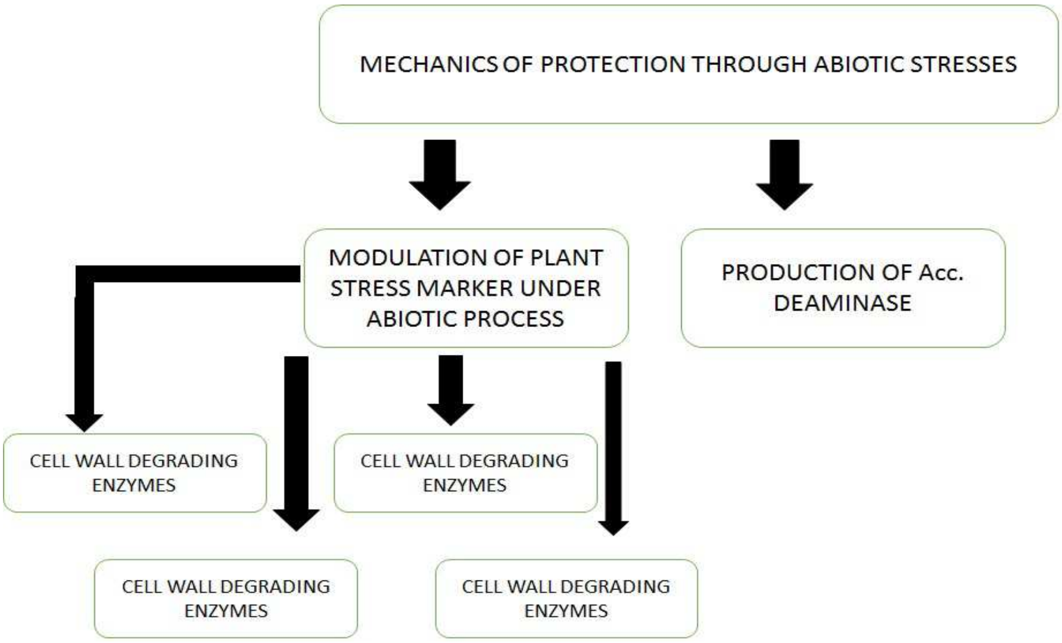

Figure 4. Mechanics of protection through abiotic stresses.

Table 3. Species responsible for antibiotic production and its probable effect [248-252].

Genus with reported strains	Antibiotic produced	Antibiotic probable effect
Pseudomonas *P. fluorescens* *P. aeruginosa*	2,4-Diacetyl phloroglucinol (DAPG), Phenazine-1-carboxylic acid (PCA), Phenazine-1-carboxamide (PCN), Pyoluteorin (Plt), Pyrrolnitrin (Prn), OomycinA, Viscosinamide, Butyrolactones, Kanosamine, Zwittermycin-A, Aerugine, Rhamnolipids, Cepaciamide A, Ecomycins, Pseudomonic acid, Azomycin, Antitumor antibiotics FR901463, Cepafungins, Karalicin	Antiviral, Antimicrobial, Insect antifeedant, Mammalian antifeedant, Antihelminthic, Phytotoxic, Antioxidant, Cytotoxic, Antitumor, PGP activities
Bacillus *B. subtilis* 168 *B. amyloliquefaciens* FZB42	Subtilin, Subtilosin A, Tasa, Sublancin Bacilysin, Chlorotetain, Mycobacillin, Rhizocticins, Bacillaene, Difficidin, Lipopeptides, Fengycin, Ituurins	Antibacterial, Antifungal, Growth inhibition of fungi, Growth inhibition in both Gram positive and Gram negative

8. CONCLUSION

PGPR since its discovery has been promising a huge part of sustainable agriculture development. But still much has to be done on both explorations as well as the implementation of PGPR. Exploration, where involves the understanding of mechanism at same time implementation, need to take care a great deal of optimization on field application. PGPR as a tool for bioremediation and biocontrol should be encouraged and preferred. PGPR has all the very potential to act as bio-fertilizer which could work in better of an ecosystem with enhancement in productivity. Looking forward to awareness, rapid research development one could soon see PGPR as a reality on large scale. Nanotechnology has been on great run seeing last few years of time. Its inclusion in the field of agriculture especially as the carrier agent, plant transformation, delivery of genetic material has long been discovered. Its application should be intensified seeing the prospect that it could lead to the reduction in damage to the ecosystem.

CONFLICTS OF INTEREST

The author has no conflict of interest to declare.

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