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Plant growth-promoting rhizobacteria: Influence to abiotic stress tolerance in rice (*Oryza sativa* L.)

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ABSTRACT

Plant growth-promoting rhizobacteria (PGPR) has been shown to govern a number of aspects of plant development, enabling the plant to survive and adapt to its surroundings, in response to unfavorable conditions that are abiotic in nature. As a staple crop, rice is particularly vulnerable to a variety of abiotic stresses including drought, salt, heavy metal toxicity, and high temperatures. In tandem, these stresses have a significant detrimental impact on rice productivity and quality. PGPR is a rhizosphere-dwelling microorganism that can improve plant development through a variety of distinctive methods, including nutrient uptake, phytohormone synthesis, modification of plant stress signaling pathways, and stimulation of stress-responsive genes. In this review, we studied the several abiotic pressures that are encountered and how PGPR can aid in resisting the stresses with a focus on rice crop, we additionally look at how PGPR minimize the dependency of agricultural soils on pesticides and chemical fertilizers. PGPR contributes to the long-term sustainability of ecosystems, plant productivity, and soil health by promoting environmentally friendly and sustainable farming practices.

1. INTRODUCTION

Abiotic stressors, or environmental stressors, are events that put plants under stress. They are the element of the ecosystem that is not biological but yet affects every living part of the system. Natural systems depend on a delicate balance, and when either of these factors is out of the ordinary, the ecosystem is stressed, endangering the health of all living creatures. Some of the main abiotic elements of the agricultural ecosystem that affect plants are water, nutrients, salts, temperature, and pH. These abiotic stresses affect both plants and microbes. Even though bacteria compete fiercely with one another,

enzyme that allows them to dissolve the cellulose cell wall of plants and allow roots to enter the apoplast, or inside the cell wall, as well as the vascular bundle-xylem, where they live and perform normal metabolic functions [1].

especially in the rhizosphere, some microbes possess the cellulase

Abiotic stressors are adverse environmental elements that limit the physicochemical qualities of soil and the functional diversity of microorganisms, leading to significant yield loss [2]. The intricate effects of climate change on the outcomes of abiotic stress pose an imminent threat to the viability and productivity of agricultural systems. The decrease in agricultural output is primarily caused by a few abiotic factors which include drought, salinity, heavy metals, flooding, and extremes of temperature [3]. The hydrological cycle is severely disrupted by high salinity drought, which is also extremely stressful and has negative effects on the environment, society, and economy [2,4]. Drought or salinity causes a variety of physiological, metabolic, and biochemical alterations in a wide range of plant species [5,6]. Decreases in respiration, photosynthesis, and protein synthesis caused by salt and osmotic stressors have a detrimental effect on the growth and development of sensitive species [7].

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Plant-associated microbes, also referred to as plant growth-promoting rhizobacteria (PGPR), are thought to stimulate plant defenses and have positive effects on plants, such as increased growth and decreased susceptibility to pathogen-caused diseases [8]. In this context, we have focused on the various types of abiotic stress that plants endure. Rhizobacteria are those essential micro-organisms that are able to help plants both directly and indirectly. The exopolysaccharide (EPS), volatile compounds, and aminocyclopropane-1-carboxylic acid (ACC) deaminase-producing plant PGPR, which is found in the rhizosphere and endorhizosphere, stimulates the production of osmolytes and antioxidants, controls the gene expression that responds to stress and modifies the morphology of the roots, resulting in plants resistance to drought [Figure 1]. For plants to thrive under drought stress, PGPR needs to promote the genes that respond to osmotic pressure and stress. In addition to enduring plants' resistance and adaptation to drought challenges, PGPR is crucial in identifying potential issues with future food security. Beyond contributing to the osmotic and metabolic changes that the PGPR treatment causes in plants, it also alters the properties of the soil to encourage plant development [9]. The phrase "induced systemic resistance," or ISR, refers to how some PGPR results in chemical or physical alterations that are considered crucial to plant defense. Although it is widely recognized that ISR produced by PGPR confers resistance against plant diseases caused by pathogens, a few published findings imply that PGPR may also function as an elicitor of abiotic stressors in plants [8]. PGPR has the capability to help plants adapt to many forms of stress and in addition PGPR has minimized the need for fertilizer and has reduced environmental pollution.

2. IMPACT OF VARIOUS ABIOTIC FACTORS ON PLANTS

Abiotic variables that are crucial include temperature, salt, drought, and heavy metals. Abiotic stressors have the potential to restrict crop yield pose challenges for crop cultivation in specific regions, and generally make conditions unfavorable. The degree of biotic stress is significantly influenced by abiotic stress. All of these stressors together have a major effect on the physiology, metabolic makeup, and gene expression of plants [10]. The disappearance of the soil microbiota might also result from abiotic stress. A sustainable approach to overcoming environmental instability and achieving agricultural

sustainability might be to replenish rhizobacteria that promote plant growth (PGPR) in an environment under abiotic stress.

2.1. Drought Stress on Rice (Oryza sativa)

Drought stress limits rice productivity and generally inhibits it from growing by negatively influencing water absorption and nutrient uptake. The rice plant's physiological, molecular, biochemical, and morphological responses are altered by drought stress. Water stress is a significant factor in the agriculture sector as it is a necessary component of cropland. Just over 60% of the 40 million ha of rice farms are irrigated. Rest is somewhat dependent on rainfall because droughts are prone to them. Drought drastically restricts rice production since crop failure is the result [11], which lowers the world's food supply. Plants with low water content may experience physiological, biochemical, and morphological damage that interferes with critical cellular processes [12]. According to Chaves et al., 2009 [13] and Zlatev and Lidon 2012 [14], the main adverse effects of drought are oxidative damage to proteins, membrane lipids, and other cell components as well as damage to the chloroplast's photosynthetic machinery. Crops may also develop more slowly, mature later, and yield grains of lesser quality in situations where there is a water shortage [12].

According to Fang and Xiong 2015 [15], drought avoidance, drought tolerance, and drought recovery are some of the many mechanisms that make up the complex quality known as drought resistance. Of note, resistance to drought is also significantly influenced by interactions with the environment [16]. As a result, the molecular basis for rice's drought resilience and the course of its evolutionary development are still unknown. Elite cultivars of irrigated rice cultivated for excellent quality and production are particularly vulnerable to drought on an individual level [17]. These comments outline a possible trade-off between production and drought resilience. If a trade-off occurs, it must be addressed when breeding for drought-resistant cultivars since it will significantly influence how rice adaptively evolves its resistance to drought. Upland rice and lowland rice are two rice ecotypes that may be distinguished based on their tolerance to drought in agroecosystems with differing soil-water conditions. Upland rice has accrued genetic diversity via adaptation to drought-prone upland locations and is grown in rain-fed, unmanaged fields, increasing its

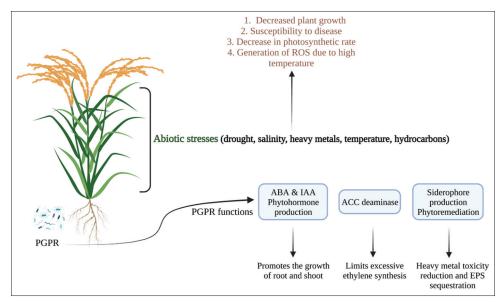


Figure 1: Plant abiotic stress tolerance and the role of plant growth-promoting rhizobacteria in plants.

drought tolerance [18] and has much stronger resistance to drought than lowland rice, as evidenced by field performance measurements conducted during drought conditions.

2.2. Effect of Soil Salinity on Plants

One of the main abiotic stresses that inhibit plant growth and yield worldwide is salinity stress. Saline soils affect about 7% of the surface area on earth [19]. Cultivable land can have its secondary salinity increased by up to 20% by inappropriate irrigation [20]. These salts can accumulate in the soil over time either through human activities or naturally such as irrigation practices and as a result, this leads to soil salinity [21]. The salinity of the soil affects almost every aspect of a plant's life, including germination of seeds, growth, uptake of nutrients and water, transpiration rate, physiological development, production, ecological balance, etc. [22]. According to Shrivastava and Kumar 2015 [21], there are several ways in which soil salinity influences plant growth. For example, saline soils have a higher osmotic potential than roots, which means that if soil salt concentrations increase drastically, plants will have less access to water. As a result, plant experiences water stress that exhibits symptoms like wilting. Saline soils also lead to nutrient imbalance, ion toxicity, disruption of soil structure, and also osmotic stress. Ions such as salt, chlorine, and boron have a deleterious effect on plants. Plant cell death due to osmotic stress may be caused by an increase in sodium ions in the cell walls [23]. Crop development processes such as microsporogenesis, stamen elongation, ovule development, and embryogenesis can be impacted by the soil's salinity, which also promotes programmed cell death [24]. Plant species vary in their tolerance to salinity, with some being tolerant and some being non-tolerant. PGPR, or beneficial bacteria that colonize the rhizosphere and improve plant growth and health, helps to lessen the detrimental effects of soil salinity on plant growth.

2.3. Effects of Heavy Metals on Rice Plant Growth

As a result of human activities such as urbanization and industrialization, heavy metals find their way into the soil. Among the dangerous and non-degradable, heavy metals that can be detrimental to plant and human health are Al, Cr, As, Cu, Hg, Pb, Se, Hg, Zn, and Mn. When humans ate rice and other grains grown on contaminated land, heavy metals seeped into the body and caused health problems. Heavy metals have detrimental effects on plant physiology, metabolism, senescence, water and nutrient absorption, growth, and physiology. It hinders the generation of plant growth hormones and damages the integrity of cell membranes, which both have an impact on plant development [25]. This results in stunted development, poor biomass, chlorosis, browning of the roots, and finally death in plants grown in heavy metal-contaminated areas. Plant absorption of heavy metals leads to a higher production of reactive oxygen species (ROS), which ultimately causes cell death. To maintain environmental sustainability, protect the ecosystem, and increase agricultural productivity, heavy metals need to be eliminated in a way that is environmentally friendly. In this sense, PGPR can promote plant growth and mitigate the detrimental effects of heavy metals on plants [26].

2.4. Impact of Temperature Stress on Rice Plant (Phytoretardation)

Among the primary abiotic stress factors influencing plant development and output is temperature, which may be either excessive or low. Nearly all of the physiological functions of the plant are impacted, reduced photosynthesis, cell division, increased transpiration, protein denaturation, and total plant development. Extreme heat increases

the fluidity of the cell membrane whereas extreme cold increases its rigidity. A higher temperature increases the generation of ROS, which may cause oxidative cell damage [27]. At low temperatures, plants exhibit obvious deterioration including wilting, necrosis, and chlorosis [28]. The content of calcium inside plant cells may fluctuate in response to temperature variations [29]. According to Ruelland and Zachowski 2010 [28], it may also phosphorylate both mitochondrial and thylakoid proteins and alter the structure of plastids and the thylakoid membrane. In all of these major problems, PGPR can assist plants in coping with heat stress and subsequently enhance plant growth development.

3. DROUGHT RESISTANCE MEDIATED BY PGPR

Rhizospheric bacteria, which naturally adapt to and live in arid environments, can aid in the growth of plants. These PGPR strains increase drought resistance in plants through a number of different processes, including ACC deaminase biosynthesis, EPS synthesis, phytohormone synthesis, and ISR [30]. When rice lacks water, phytohormones such as abscisic acid (ABA) and IAA are released by PGPR stimulating the growth of the shoots and roots. Drought tolerance genes are activated and hydraulic conductivity is increased by phytohormone ABA, which reduces the stress brought on by drought. Belimov et al., 2001 [31] state that the enzyme ACC deaminase, which generates PGPR, can promote plant growth in rice plants exposed to unfavorable climatic conditions by limiting the synthesis of excessive ethylene by converting ACC, an ethylene precursor, into ammonia and F-ketobutyrate. Further, the synthesis of sugar, amino acids, water, and proline is increased by PGPR inoculation, which also increases the plant's biomass and water potential [32]. Plants under Pseudomonas putida treatment experience less stress from dry circumstances because their levels of biomass and chlorophyll are higher [33]. The combined application of mycorrhizae and PGPR may help to mitigate the harmful impacts of drought. A brief description of the PGPR strains that have been used in O. sativa and have demonstrated tolerance to abiotic stress is listed in Table 1.

4. PGPR'S SALINITY-REDUCTION MECHANISM

The stress of salt on plants can be reduced using rhizobacteria that promote plant development PGPR. It reduces stress and promotes plant development both indirectly and directly. Nutrient mobilization, siderophore synthesis, phytohormone synthesis, and nitrogen fixation are a few of the direct mechanisms [34]. While the indirect method

Table 1: List of few researches that explored *Oryza sativa's* ability to withstand abiotic stress using the PGPR strains.

Crop	Abiotic stress	PGPR	References
Oryza sativa	Salinity	Alcaligenes faecalis Bacillus pumilus Ochrobactrum sp. Pseudomonas pseudoalcaligenes	[68,69]
	Drought	Osmotolerant bacteria Consortia containing Pseudomonas jessenii, R62, Pseudomonas synxantha, R81 Arthrobacter nitroguajacolicus strainYB3, strain YB5 Azospirillum brasilense Az39	[70-72]
	Heavy metal	Bacillus subtilis Bacillus megaterium Bacillus sp.	[73]

entails keeping a variety of plant pathogens from infecting plants. PGPR not only helps convert ACC into α -ketobutyrate and ammonia but also produces the enzyme ACC deaminase, which prevents plants from producing excessive ethylene. By controlling the production of rhizobitoxine enzyme in salt-challenged conditions, it also promotes the development of root nodules in plants [35]. According to Kasim *et al.*, 2016 [4], the EPS generated by the PGPR functions as an inhibitor that binds with the cations and aids in the plant's reduction of salt stress.

Many rhizobacteria have PGPR characteristics that enable them to resist salt stress. According to Bano and Fatima, 2009 [36], Pseudomonas and Rhizobium bacteria are helpful for fostering plant growth in salt. It has been observed that inoculating rice plants with Pseudomonas pseudoalcaligenes and Bacillus pumilus inhibits the activities of superoxide dismutase and lipid peroxidation under salt stress [37]. In addition, they increased the rice plant's ability to produce glycine betaine and made it more resistant to salt [38]. Bacillus subtilis and B. pumilus promote the growth of plants in saline soil by solubilizing phosphate and producing HCN, IAA, and ammonia [39]. Rice plants become salt-resistant due to the production of phytohormones such as auxins and ABA by Bacillus amyloliquefaciens, as reported by Shahzad et al., 2017 [40]. According to Nautiyal et al., 2013 [41], the B. amyloliquefaciens bacterium is necessary for the regulation and repression of 14 different rice plant genes to mitigate the impact that saline stress has on rice plants.

5. HEAVY METAL SEQUESTRATION VIA PGPR MECHANISM

When plants are under significant metal stress, PGPR might accelerate plant growth. PGPR reduces the toxicity of heavy metals by several methods, such as detoxification, volatilization, heavy metal efflux, limiting metal entrance into cells, and complex formation. Furthermore, PGPR reduces the synthesis of ethylene while stimulating the synthesis of other plant growth regulators, such as ACC deaminase and IAA [42]. PGPR facilitates plant development by mobilizing essential nutrients, solubilizing phosphorus, fixing atmospheric nitrogen, and producing siderophore [43]. According to Zhang et al., 2020 [44], phylum Actinobacteria and Proteobacteria are used for the removal of As, Mn, and Pb from polluted soil. Cu phytotoxicity decreased when PGPR was applied to the agricultural plants [45]. Cadmium is mobilized from contaminated soil by Klebsiella sp. and Micrococcus sp. and encourages plant growth by lengthening their shoots and roots [46]. Arsenic is incorporated into biomass by certain bacteria such as Azospirillum brasilense and Bradyrhizobium japonicum, which also promotes plant growth and development when exposed to heavy metal stress [47].

A novel approach called "phytoremediation" refers to using plants to extract heavy metals from soil. Micro-organisms are utilized in phytoremediation to boost its effectiveness and create a biomarker for heavy metal pollution [48]. According to Babu et al., [49], certain bacteria can eliminate metal contaminants from the environment, while other bacteria can change the highly poisonous form of the metal ion into a less hazardous one. Heavy metals are detoxified by Pseudomonas spp. in the biotransformation of cadmium citrate and the Fe (III)-Zinc complex [50]. According to Saha et al., [51], bacteria-produced siderophore chelate additional metals in addition to ferric ions and aid in phytoremediation. As a result, PGPR promotes plant growth by alleviating the impacts of heavy metal stress.

6. INFLUENCE OF PGPR ON THE MECHANISMS UNDERLYING THERMOGENIC STRESS AND ADAPTATION

Thermogenic stress refers to the adverse effects of high temperatures on plants, which might eventually lead to biochemical or physiological disruptions. By utilizing micro-organisms that encourage plant development, plants can be protected from the harmful effects of thermic stress. As they are ubiquitous, microbes can be used as a tool to promote the growth of plants in a variety of temperature circumstances. Under extremely cold conditions, psychrophilic bacteria such as Arthrobacter nicotianae, Brevundimonas terrae, and Pseudomonas cedrina showed the ability to promote plant growth and development [52]. The effectiveness of psychrophilic bacteria in boosting plant development and their antibacterial activity has been the subject of several publications [53,54]. Similarly, research on thermotolerant bacteria that can produce organic acids to convert phosphate from an insoluble form to a soluble state has been conducted for a very long time [55]. Plants develop their own osmolytes, polyphenols, and other secondary metabolites that help them cope with temperature fluctuations and prevent oxidative damage to plant cell membranes at high temperatures [56].

Plants can also produce antioxidants like glutathione to protect cells from the damaging effects of ROS. Under circumstances of high temperature, the bacteria *Paecilomyces formosus* demonstrated features that promoted plant development. Comparable to bacteria, endophytic fungi and other symbiotic fungi, such as *Curvularia protuberata*, enhanced plants' ability to tolerate heat and had an impact on their development [57,58]. Furthermore, it is critical to note that the capability of the bacterial strain, the surrounding environment, and the type of plant species all affect PGPR in thermogenic stress adaptation. Collectively use of PGPR reduces the detrimental effect of high temperatures on plant growth and promotes adaptability so that plants may survive in thermogenic stress environments [26].

7. CHALLENGES AND LIMITATIONS OF PGPR IN RICE PLANT ABIOTIC STRESS TOLERANCE

Rhizobacteria that encourage plant growth have been extensively researched for their potential to improve abiotic stress tolerance in plants. However, the usage of PGPR is not without its difficulties and restrictions. Below is a list of the majority of them.

7.1. Variability and Strain Specificity

Different PGPR strains have variable impacts on the capacity of rice plants to withstand stress, and environmental conditions can affect how well they work. It can be difficult to identify and choose the best strains for certain abiotic stressors and then optimize their use [59]. All PGPR strains will not be equally effective in promoting stress tolerance to rice plants.

7.2. Interaction with other Micro-organisms

The performance of PGPR may be impacted by the presence of other microbes in the rhizosphere. The colonization and advantageous effects of PGPR in rice plants may be constrained by competition or antagonistic interactions with other micro-organisms [60].

7.3. Inconsistent Performance

The efficacy to which PGPR improves rice's abiotic stress tolerance varies under different field conditions, making it challenging to achieve

consistent results. Factors such as soil type, climatic conditions, pH, nutrient availability, and agronomic practices can influence the performance of PGPR [61].

7.4. Lack of Standardized Protocol and Limited Understanding of the Mechanisms

There is a lack of standardized protocols for the isolation, characterization, and application of PGPR strains for abiotic stress tolerance in rice. This hinders the comparability of results across different studies and makes it difficult to identify the most effective strains and application methods [61].

7.5. Field-scale Application and Cost-effectiveness

Scaling up the application of PGPR in rice fields can be challenging due to the cost of production, formulation, and application methods. Developing cost-effective and practical strategies for large-scale applications is essential for their widespread adoption [62].

7.6. Compatibility with Other Inputs

The compatibility of PGPR with other agricultural inputs, such as fertilizers, pesticides, and fungicides, needs to be considered, as some of these inputs may interfere with PGPR colonization and growth or affect their efficacy in improving abiotic stress tolerance [8].

8. FUTURE PERSPECTIVES

Several studies indicate the potential of PGPR to enhance the growth of rice plants and stress tolerance. For example, B. pumilus, a commonly studied PGPR, was found to promote tolerance to rice plants against salt stress by lowering Na+ accumulation in plant tissues and enhancing antioxidant enzyme activity [63]. Similarly, it has been found that B. subtilis increases rice tolerance to drought stress through enhanced osmotic adjustment and water usage efficiency [64]. In addition, it has been found that PGPR increases the uptake of nutrients in rice plants, which can further improve their stress tolerance. For instance, a wellknown PGPR, A. brasilense was found to enhance nitrogen uptake and promote root growth, which improves rice growth and drought tolerance [65]. Overall, the application of PGPR in the cultivation of rice shows great promise for improving plant development and stress tolerance, which would ultimately result in higher yields and a more secure food supply. More research is required to fully comprehend the mechanisms through which PGPR promotes plant development and stress tolerance to maximize its use in rice cultivation. Further, the rice plant's resistance to drought stress was enhanced with the application of PGPR spraying. The researchers discovered that plants treated with PGPR strains had more antioxidant activity and suffered less oxidative damage in areas that experienced drought [66].

Similar results were found in another study by Khan *et al.*, 2020 [62] which showed that PGPR inoculation increased rice plants' ability to tolerate salt. Under salt stress, the researchers found that plants treated with PGPR developed more roots, had more chlorophyll, and were less harmful to ions. Further studies were performed to look at the potential of PGPR to minimize the negative impacts of heavy metal stress on rice plants, where many scientists discovered that PGPR inoculation enhanced the plants' antioxidant defense mechanisms and reduced the accumulation of heavy metals in plant tissues [67]. The results of these studies suggest that the application of PGPR may improve rice plants' resistance to abiotic stress. Further, to fully understand the mechanisms behind the beneficial effects of PGPR

on plant stress responses, more research is needed to maximize their application in agricultural environments. In conclusion, PGPR holds great promise for sustainable agriculture, crop yield improvement, and environmental conservation at the same time.

9. CONCLUSIONS

The comprehensive and current research information on the effects of PGPR on rice plant resistance to abiotic stress is presented in this review. The study results mentioned throughout the paper offer strong support for the idea that PGPR can significantly enhance rice plants' resilience to and ability to adapt to a variety of abiotic stimuli. The significance of abiotic stresses in influencing rice plant growth and productivity was underlined in the article. Drought, salinity, and temperature extremes are some of the challenges that PGPR encountered. Given that these pressures pose significant challenges to the cultivation of rice, finding workable solutions to decrease their negative impacts is crucial for sustainable agriculture. Future PGPR research has a wide range of potential applications, including combining it with other biofertilizers or bio-pesticides to increase their overall potency as well as commercial development of effective PGPR products. Therefore, more extensive research is required to find and characterize the noble PGPR strains with enhanced features as well as to comprehend the full mechanisms by which PGPR interacts with plants and encourages vital growth.

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11. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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14. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

15. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

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