



## Phosphate solubilizing bacteria and their protective role against environmental stressors

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### Abstract-

The continuous population boom has made us heavily reliant on the agricultural sector to meet our nutritional requirements. The global agricultural output however faces several challenges. The lack of phosphorous as a nutrient and the presence of various stressors in the environment are the major of these challenges. Phosphorous is an essential macronutrient responsible for overall plant growth and development. However, despite their abundance in soil, they remain inaccessible to plants because of their insoluble nature. Traditional methods of availing this inaccessible phosphorous such as chemical phosphate fertilizers have adverse effects on the environment, so alternative methods are sought. To tackle this issue, phosphate solubilizing bacteria were introduced which possess the ability to convert insoluble forms of phosphorous into their soluble forms which become available to be utilised by plants. These phosphate solubilising bacteria are also capable of offering protection against the various stressors plaguing the global crop supply such as salt stress, drought stress, temperature stress, pH stress and heavy metal stress. Therefore, utilizing phosphate solubilising bacteria as bioinoculants serves to potentially tackle both the lack of soil phosphorous and the presence of various stressors. This review deals with the major stressors that affect the global crop supply and the various phosphate solubilising bacteria that are employed to bio-protect such crops in order to maintain the global crop output.

**Keywords-** Phosphate solubilising bacteria, plant growth promoting rhizobacteria, salt stress, drought stress, heat stress, cold stress, heavy metal stress

### Introduction-

Phosphorous is one of the most important nutrients required for sustaining all life on Earth. It is a structural component of human and plant nucleic acids and aids in cell division and physiological reactions. Deficiency of phosphorous can lead to major problems including a loss of appetite and bone soreness in humans. Meanwhile in a phosphorous deficient environment, plants suffer from stunted growth and development. Despite their abundance in

the ground, phosphorus remains inaccessible to plants and animals. Previously, chemically produced phosphate fertilizers were used to meet the phosphorous needs of plants, but this practice typically has unfavourable effects on the habitat (Yadav, 2022). To meet the phosphorous demand of plants without the introduction of chemical phosphate fertilizers into the environment, innovative and environmentally acceptable alternatives are required.

The majority of phosphorous in the soil is insoluble and present in organic and inorganic forms. This unavailability results from phosphorous-fixation, which occurs when phosphorous is either adsorbed on soil minerals or precipitated by free  $\text{Fe}^{3+}$  and  $\text{Al}^{3+}$  in the soil solution which renders it unusable for plants (Sharma et al., 2013). When phosphorous is supplemented to the soil, its availability to plants rapidly increases. However, a significant portion of this phosphorous immediately gets transformed into its insoluble form, leaving behind a minute portion accessible to plants. This necessitates the continuous administration of fertilizers.

Therefore, in order to maintain a steady supply of available phosphorous for plants, there has been a constant requirement for the repeated application of phosphatic fertilizers. Most phosphatic fertilizers however, contain various heavy metals (Azzi et al., 2017). This leads to their accumulation in the soil which has a negative impact on soil fertility, animal and consumer health, eutrophication, and an ever-growing carbon footprint (Huang et al., 2017). Given the situation, a green strategy that may accomplish the same purpose as synthetic fertilizers without the accompanying drawbacks is urgently required.

There has been a substantial, ongoing effort to seek alternative methods of increasing phosphorous availability and solubilization. Live microorganism used as bioinoculants and biofertilizers called phosphate solubilizing microorganisms (PSMs) are promising alternatives to traditional agrochemicals. PSMs are responsible for improving the soil fertility by making the primary nutrients like nitrogen and phosphorous available to host plants.

Another link in favour of using PSMs as bioinoculants is the protection they offer against various stressors. Various abiotic and biotic stress conditions cause damage to plants during every stage of development which significantly reduces their yield. This reduction in yield causes significant damage to the global crop supply. The presence of such stressors also significantly impacts the establishment and performance of PSMs, which makes it pertinent to isolate microorganisms with good phosphorous-solubilizing abilities from these conditions such as saline or alkaline soil (Sharan et al., 2008). The efficiency of phosphate-solubilizing

bacteria (PSB) is governed by various elements linked to the interaction of the plant and bacteria.

From an agricultural viewpoint, under changing climatic conditions, systematic identification of bacterial strains offering cross-protection against different stressors would be extremely beneficial. A plant can be bio-protected against biotic stressors by being injected with non-pathogenic bacteria, while some root-colonizing bacteria boost resistance to abiotic conditions like drought, heavy metal toxicity, and salinity. Understanding the underlying physiological, morphological, and molecular mechanisms of bacterially mediated stress tolerance is essential for bacterial cross-protection to be employed as a useful tool (Dimkpa et al., 2009).

### **Phosphate Solubilizing Bacteria-**

Among the PSMs, the bacteria possessing the capacity to solubilize phosphate are called phosphate solubilizing bacteria (PSB). These microorganisms solubilize phosphorous for their own needs as well as to satisfy the plant's phosphorous requirement. PSBs are capable of maintaining a supply of phosphorous by various methods, the three main methods among these are solubilization, mineralization, and immobilization (Kour et al., 2021).

Employing PSMs as bioinoculants can provide a sustainable alternative to accomplish the same goals as chemical fertilizers, thereby lowering the dependence on such fertilizers (Kour et al., 2020). Several soil microorganisms exhibit the capacity to solubilize dicalcium phosphate (DCP), tricalcium phosphate (TCP), and hydroxyapatite (HAP), generally by releasing phosphorous from the soil by secreting mono-, di-, or tricarboxylic acids which are most effective in dissolving calcium phosphate (CaP) complexes (Padmavathi, 2015). These microorganisms have been thought to be important in providing phosphorous to plants, especially those that thrive in specific soil conditions, such as alkalinity and salinity, where CaP complexes are twice as high.

Numerous soil plant growth-promoting rhizobacteria (PGPR), including PSB inhibit a variety of plant pathogens and enhance plant growth through a variety of mechanisms, including the direct and indirect production of various phytohormones, decomposition of organic matter, as well as an increase in the bioavailability of various mineral nutrients like iron and phosphorous (Saeed et al., 2021). PSBs are usually associated with the genera *Bacillus* and *Pseudomonas*. They are thought to reside in the rhizosphere and are generally used as

inoculants for bio-stimulation, biocontrol, and biofertilization. Some bacterial strains produce siderophores and employ them as bio-controlling agents by preventing various phytopathogens from accumulating iron and inhibiting their growth (Numan et al., 2018). Gibberellins (GA), indole acetic acid (IAA), abscisic acid (ABA), cytokinin (CK), cofactor pyrroloquinoline quinone (PQQ) and ethylene are just a few of the hormones that enhance plant growth are activated by PGPR (Sahu et al., 2017).

### **Environmental stressors against plants and the protective role of phosphate solubilizing bacteria:**

In a world with expanding population and rising food prices, abiotic stress factors like drought, extreme (high/low) temperatures and salinity are recognized as the primary causes of crop output losses. Limited nutrient availability and notably poor phosphorous soil status coupled together with stressors have an adverse effect on overall plant health. In light of this, finding a resource with the ability to make the unavailable deposit of phosphorous in soil accessible to plants as well as provide protection against the different stressors can tremendously help in increasing the global crop output. A few of the major stressors which plague the global crop supply are discussed in the upcoming sections.

#### **Salt stress-**

About 5.2 billion hectares of fertile land is affected by salinity, erosion and soil degradation causing enormous problems for farmers. About 50% of these areas are affected by salinity stress alone (Riadh et al., 2010). Salt stress can be defined as the osmotic forces exerted on plants when growing in salt marshes or other excessively salty conditions. The accumulation of carbonates ( $\text{CO}_3^{2-}$ ), bicarbonate ( $\text{HCO}_3^-$ ), sodium (Na), sulphate ( $\text{SO}_4^{2-}$ ), calcium (Ca), magnesium (Mg), potassium (K), chloride ( $\text{Cl}^-$ ) and other salt ions in soil is called salinization. Sodium chloride is the main component of most salts, and its chloride ions are toxic to plants, and at high concentrations said to retard plant growth (Ruan et al., 2010).

Salinity significantly diminishes agricultural acreage every year which has a negative socio-economic impact on food production. Plant development and metabolism is negatively impacted by the high concentration of sodium ions in plant tissue present in saltwater environment. In addition to reducing flowering, salinity also reduces the yields of various crops. It reduces grain yield and seed by affecting pollination (Machado & Serralheiro, 2017).

Salt tolerance is the ability of plants to grow in saline conditions despite the adverse effects of high salt concentrations. Plants develop different mechanisms of salt tolerance like hormone modulation, biosynthesis of compatible solute and osmoprotectants, antioxidant enzyme activation, antioxidant compound synthesis, ion uptake and transport, polyamine production, ion homeostasis and nitric oxide production (Numan et al., 2018).

Arginine, cysteine, and methionine account for 55% of the total amino acids and have been reported to decrease with salinity exposure, while proline demonstrates a reported increase in concentration. Proline accumulation is a known measure used to reduce salinity (Ben Ahmed et al., 2010). Proline accumulated during salt stress confers tolerance and is an important source of organic nitrogen during stress (Saxena et al., 2013).

More than 60% of the world's land surface is affected by salt; the majority of this salt-affected land was created by natural processes and the long-term deposition of salt in arid and semiarid regions. Salinity in the soil prevents plants from absorbing water from the soil by causing osmotic stress, ion toxicity, oxidative stress, and nutritional (N, Ca, K, P, Fe, Zn) deficiencies (Artiola et al., 2019).

In saline soil, these issues are typically resolved by using techniques like addition of organic matter such as sewage sludge, farmyard manure and modified biochar (Ding et al., 2020). Unfortunately, these mitigating strategies have drawbacks and have a deleterious impact on soil like causing unfavourable changes in the soil's physical, chemical, and biological properties as well as the accumulation of toxic heavy metals (Dey et al., 2021). It was discovered that PSB isolates generally demonstrated the potential of phosphate solubilization up to 70% NaCl concentration, and that colony expansion was seen even at higher NaCl concentration without the presence of a halo zone of clearing (Mohan et al., 2017; Sharan et al., 2008).

Hypersaline conditions harm the plant in more ways than one. It has been observed that salinity disrupts the normal physiology and biochemical processes of the plant and makes it susceptible to infections. According to some studies, salt-tolerant phosphate solubilizing bacteria (ST-PSB) may help provide resistance against the various phytopathogens and provide an added layer of protection against infections. The phytopathogens are resisted by ST-PSB via several methods. Rhizobacteria that produce siderophores have been discovered as possible biocontrol agents for preventing or lowering pathogen's proliferation and controlling plant illnesses. ST-PSB produces a lot of siderophores which may actively

contribute in controlling phytopathogens by taking away the soil iron which remains essential for microbial growth (Olanrewaju et al., 2017; Pandey & Gupta, 2020).

There are multiple methods by which ST-PSB can potentially control pathogen outbreak. ST-PSBs produce various enzymes such as fungal cell wall-degrading enzymes like chitinase and lipase which can break down the lipid-associated with fungal cells and protease, which can break down the associated protein in the cell wall of the fungus. Chitin is an essential component of the fungal cell wall and its breakdown leads to cell lysis and death, thereby preventing the onslaught of fungal infection (Bouizgaren et al., 2013).

### **Drought stress-**

Drought is a major environmental condition that hurts the agricultural sector globally. In 50% of the world's dry or semiarid terrain, groundwater levels are scarcely available to the local plants. Since water is such an essential component of the regular functioning of the plant metabolic activities, this lack of water leads to dehydration of plant cell and a stressful condition known as drought stress. Drought stress affects the biochemical, morphological, and physiological processes that normally occur in plants by restricting leaf size, nutrient intake, stem extension, root proliferation and the relative water content (Hidayat, 2019; Kang et al., 2021).

The frequency of extreme drought conditions is rising due to the constant rise in temperature and water scarcity (Salim et al., 2019). Crop plants under drought stress have poor development, growth and productivity due to a reduction in the availability of nutrients. By increasing metabolite flux and producing reactive oxygen species which increase the oxidative load and severely damage biological macromolecules, drought stress also results in membrane damage and stomatal closure (Osakabe et al., 2014).

According to several recent studies, adding PSMs that promote plant growth in the plant-soil system lessens the adversity brought on by drought stress (Vassilev et al., 2012). In a study using multifunctional *Azospirillum* species, including those with phosphate-solubilization activity, it was shown that adding more helpful microorganisms to the soil during drought stress increases the overall number of bacteria compared to the uninoculated control treatment, showing that bacteria can survive drought stress due to plant adaptation, which is in turn made possible by the presence of *Azospirillum*. Some scientists also used different plants to demonstrate the impact of five drought-tolerant *Pseudomonas* strains that exhibited

traits that encourage plant growth and production of siderophore, IAA, gibberellins along with a marked phosphate solubilizing activity (Sandhya et al., 2010). Previously published isolates from drought-tolerant plants solubilized more phosphorus under stress compared to regular conditions, making PSBs more popular as phosphate biofertilizers owing to their cost-effectiveness and environmental sustainability alongside their phosphate solubilizing activity even in drought stress (Arzanesh et al., 2011; Bouizgaren et al., 2013; Kang et al., 2021).

### **Temperature stress-**

A key abiotic stress that influences plant life, geographic spread and yield on a worldwide scale is temperature stress. Plants adjust their morphological, physiological and metabolic pathways and cellular and sub-cellular structures to cope with temperature stress through signal transduction and the expression control of temperature stress-related genes (Huang et al., 2017; Kim et al., 2015).

Extreme temperature conditions put plants under stress. As an illustration, root elongation occurs only above a specific, species-dependent minimum temperature and grows virtually linearly with rising temperature until a particular maximum temperature, at which point the elongation rate sharply declines. High temperatures have a strong negative impact on photosynthesis while low temperatures will damage many essential parts of the photosynthetic apparatus (Greer & Weedon, 2012; Tan et al., 2011).

Agriculture production systems are vulnerable to shifting environmental circumstances in an era of global warming. It has been demonstrated that root-colonizing bacteria can boost the tolerance of host plants to abiotic stimuli and can mediate as well as enhance resilience to biotic stressors. So, it would be extremely beneficial to identify certain bacterial strains that can concurrently provide cross-protection against a number of stress factors. Temperature stress and the related tolerance mechanisms have been discussed further in the upcoming sections under the headings of cold and heat stress.

## **Cold stress-**

It was discovered that agriculture has several significant obstacles in various hilly places of the world. Cold temperature and low fertility are the major causes among these. Due to the direct suppression of metabolic enzymes by cold stress and the programming of gene expression, cold stress can harm a plant by lowering photosynthetic rates (Al-Busaidi et al., 2012). It has been discovered that using commercially available biofertilizers in cold conditions, such as those prevalent in mountainous locations remains unsuccessful in tackling these issues.

Over the past 20 years, several biotechnological and microbiological strategies utilizing organisms that are either cold-loving or cold-tolerant have been tested to overcome these difficulties (Yarzabal, 2014). According to their capacity to thrive at low temperatures, which may range between 0-20°C and 0-35°C, cold-tolerant soil microorganisms are classified as either psychophilic or psychrotrophic respectively (Vassilev et al., 2012).

A team of Indian scientists conducted one of the first research on cold-tolerant phosphate-solubilizing microorganisms to address the need to choose beneficial soil bacterial strains from the high-arctic and low-temperature zones of the Indian Himalayan Region (Das et al., 2003). It has been demonstrated that the process of phosphate solubilization can be accompanied by the generation of organic acid, various plant stimulants, enzymes, and biocontrol activity.

Similar experiments using *Acinetobacter rhizosphaerae*, a bacterium isolated from the frigid deserts of the Himalayas, showed the bacterium's multifunctional capability and high competence in promoting plant growth. High inorganic and organic phosphate solubilization activity was demonstrated by the wild strain and its mutations (Gulati et al., 2009). In controlled environments, *A. rhizosphaerae* increased root length and dry matter in maize, barley, peas, and chickpeas, compared to unvaccinated controls in field conditions.

In the mid-to-late 1990s scientists acquired cold-tolerant mutants of *Pseudomonas fluorescens*, a well-known PGPR species capable of solubilizing phosphorous and assessed their impact on plant growth promotion at low temperatures. The mutants were created by treating three separate *P. fluorescens* strains- GRS1, PRS9, and ATCC13525 with nitrosoguanidine (Dash et al., 2019; Mohammed et al., 2011). Some scientists demonstrated that some of these *P. fluorescens* mutants could solubilise significantly more phosphorous at 10°C than their respective natural strains. This original work was supplemented by a second



investigation that showed two of these mutants might improve both in-situ and in-vitro growth of wheat and mung bean growth at 10 °C.

Some of the most remarkable bacterial species that have been isolated thus far from natural soils of alpine and sub-alpine locations and tested for both their resistance to low temperature and their effectiveness in dissolving inorganic phosphate are *Pseudomonas putida*, *Bacillus megaterium*, *Acinetobacter rhizosphaerae*, *Mycobacterium phlei*, *Achromobacter* sp., *Tetrathlobacter* sp., *Bacillus subtilis*, *Rahnella* sp., *Pseudomonas corrugata*, *Pseudomonas lurida*, *Pseudomonas fragi* and *Serratia marcescens* (Saeed et al., 2021).

The cold-tolerant PSB is a diverse group that encompasses species from both distantly related and closely related genera of Gram-positive and Gram-negative bacteria. *Pseudomonas* has been found and tested as the most pertinent cold-tolerant PSB followed by *Bacillus* species (Yarzabal, 2014).

### **Heat stress-**

During high-temperature conditions, heat shock proteins (HSPs), which are abundantly present in fungi, mammals and plants, may be crucial in the body's reaction response to heat stress. It may enhance the generation of reactive nitrogen species (RNS), which harm cells and cause nitrosative stress (Corpas et al., 2011; Groß et al., 2013). The equilibrium between the synthesis and removal of reactive oxygen species (ROS) is drastically upset. Increasing amounts of ROS can chemically modify or render inactive proteins, lipid membranes, and DNA (Zhang et al., 2017). High levels of ROS including H<sub>2</sub>O<sub>2</sub> and O<sub>2</sub> are generated in seedlings in situations with severe temperatures, which causes a rise in membrane permeability, protein breakdown and the loss of other cellular components (Martinez et al., 2018).

Cellular phospholipid membrane fluidity can be altered by both cold and heat stress. Integral membrane proteins are capable of detecting a kind of alteration, which enables stress transcription factors to activate stress-responsive genes (Scharf et al., 2012). Eventually, these pathways result in a modification to plant metabolisms and growth that are intended to achieve homeostasis under challenging circumstances. Similar research has demonstrated that exposure to high temperatures can cause either excessive or sluggish growth, as well as a decrease in the relative water content of seedling leaves. High-temperature stress causes stomatal closure, which causes a decrease in CO<sub>2</sub> utilization, which causes a fall in photosynthetic rate (Ahanger et al., 2014; Al-Busaidi et al., 2012). Therefore, identifying and

isolating microbial strains like PSBs and PGPRs from the soil facing heat stress becomes important in overall plant protection.

### **pH stress-**

During summer, many places in India experience high salt, high temperature, and high pH load on bacteria thriving in alkaline soils. Temperature can vary from 35-45 °C in the alkaline soils of the tropics, where salt concentrations can reach 2% and pH can reach 10.5 (Alexandre & Oliveira, 2011). In semi-arid and dry areas of the world, PSB could increase the production of food and forage due to its genetic potential for increased tolerance to high salt, high temperature and high pH.

The ability of bacterial strains to reproduce, survive and disseminate in alkaline soil under high salt and high pH conditions may be crucial. Osmotic, pH, and temperature-stressed habitats are likely to contain microorganisms that can withstand stress. Recently, some scientists have developed a defined medium for PSB screening and created a method for the majority of effective phosphate solubilizers in soil (Abdul Rahman et al., 2021). They isolated four bacterial isolates using this technique: NBRI0603, NBRI2601, NBRI3246, and NBRI4003. The other three isolates were obtained from various alkaline soils, while strain NBRI0603 was isolated from the rhizosphere of chickpeas growing in alkaline soil. Regarding phosphorus solubility in the presence of the 10% salt, pH 12, or 45 °C, NBRI2601 was the most effective strain among the four (Nautiyal et al., 2000).

### **Heavy metal stress-**

Heavy metals are dangerous for plants, animals and bacteria because they directly impact our ecosystem in general and the agroecosystem in particular. Heavy metal pollution of the biosphere has been observed at a global scale (Yeo & Langley-Turnbaugh, 2010). Bioremediation is one of the most prevalent, affordable, and environmentally friendly methods that can be used to successfully address this issue (Dash et al., 2019).

Globally, soil pollution from hazardous heavy metals has increased as a result of rapid urbanization and industrialization. Heavy metals pose a concern to human health because they are easily concentrated by plants and animals, are difficult to degrade in the environment and are amplified by biomagnification (Zhang et al., 2017).

The second largest issue for academics after soil contamination is heavy metal pollution of the atmosphere. Anthropogenic sources release about 30% of the world's annual mercury

emission into the atmosphere, with Asia accounting for 50% of this total (Sundseth et al., 2017). As they are persistent, heavy metals build up in our bodies and cause a number of health problems (Garg et al., 2014). Our bodies absorb heavy metals from food, drink, and the environment. However, the primary route by which heavy metals enter our bodies is through food (Yadav et al., 2017). Anthropogenic activities that pollute soils with heavy metals (HM) pose a serious risk to plant viability all over the world. However, through sophisticated physiological features, metabolic pathway adaptations, and interaction with helpful bacteria, several plant species may thrive in this environmental circumstance (Xu et al., 2015).

Like all other living forms, microorganisms are stressed by heavy metals. Diatoms and microalgae are commonly employed as bioindicators and for assessing heavy metal pollution (Đukić & Mandić, 2006). Even at species and strain levels, they show signs of being extremely vulnerable to heavy metals. Different habitats and kinds of microbes have varying levels of tolerance to heavy metals. The process of microbial biosorption, which involves certain metabolic or physiochemical pathways allow microorganisms to uptake heavy metals. The physiochemical state of the cell, the characteristics of the growth media and the type of microorganisms growing all play a role in the rate of this heavy metal uptake (Vijayadeep, 2014).

The chemical process by which an organism alters chemicals such as nutrients, amino acids, toxins, and drugs is known as biotransformation. The carbon source and pH are the two most important factors in heavy metal biotransformation in soil. One of the better changes for the bioremediation of heavy metals in the rhizosphere is through plant growth-promoting rhizobacteria. Biotransformation is another way for microbes to demonstrate resistance to heavy metals. The bioremediation of heavy metals is more productive and effective when rhizobacteria modify plant metabolism in response to heavy metal stress, enabling plants to resist high metal concentrations (Hartmann & Six, 2023).

Among all of these heavy metals, arsenic is listed by WHO as one of the 10 most dangerous substances. Regular use of food tainted with arsenic poses a direct hazard to one's life. One of the primary sources of arsenic pollution in the soil is agricultural herbicides. These compounds allow a total of 80-90% of the arsenic produced each year to enter the soil (Tchounwou et al., 2012).

Lead, a dangerous heavy metal, combines with phosphate to generate a stable compound. Lead poisoning can have a negative impact on the nervous system, the liver and kidney system, and hematological function as well as cause catastrophic illness and high migraine (Wani et al., 2015). By immobilizing lead with insoluble phosphorous sources, selected PSB can be used to photostabilize lead-contaminated soil, preventing environmental degradation brought on by the use of soluble phosphate sources for Pb immobilization. This is accomplished by solubilizing insoluble phosphorous sources which in turn promotes plant growth (Hidayat, 2019).

The main remediation techniques of heavy metals now involve stabilizing and immobilizing hazardous heavy metals in the soil in order to prevent lead or cadmium from being absorbed by plants, particularly crops (X. Zhang et al., 2017). This stabilization and immobilization can be attained by using various PSBs and PGPRs. For instance, *Lepidium sativum* plants and rhizospheric *Azotobacter* bacteria are utilized to restore damaged soil from cadmium and chromium contamination (Sobariu et al., 2017). Rhizobacteria such as *Bacillus megaterium* and *Pseudomonas aeruginosa* isolated from the weed *Suaeda nudiflora* growing in chemically polluted locations were responsible for the bioremediation of zinc (Chang Lee et al., 2018). Gram-negative Rhizobacteria including *Rhizobium radiobacter*, *Rhizogenes*, *Enterobacter asburiae*, *Agrobacterium radiobacter*, *Sphingomonas paucimobilis*, *Pantoea* sp. and gram-positive Rhizobacteria like *Bacillus megaterium*, *Bacillus pumilus*, *Bacillus cereus*, *Arthrobacter globiformis*, and *Staphylococcus lentus* are the microbes which help to inhibit arsenic contamination (Titah et al., 2014). *Arthrobacter*, *Flavobacterium* sp., *Burkholderia* sp., and *Pseudomonas* sp., are significant genera of cadmium-resistant rhizobacteria reported from some food crops maize, pumpkin, barley, mung bean, black gram, and wheat (Saluja & Sharma, 2014). A comprehensive description about the use of various bacterial inoculants to provide protection against different environmental stressors in plants is given in table 1.

Table 1: Plant tolerance to various abiotic stressors mediated by bacteria.

| <b>Stressor</b> | <b>Plant species</b>                      | <b>Bacterial inoculate</b>  | <b>Reference</b>                   |
|-----------------|---|---|------------------------------------|
| Salt            | Pea ( <i>Phaseolus vulgaris</i> )         | <i>Azospirillum brasilense</i>  | (Dardanelli et al., 2008)          |
| Salt            | Maize ( <i>Zea mays</i> )                 | <i>Pseudomonas syringae</i> ,<br><i>Pseudomonas fluorescens</i>                                   | (Nadeem et al., 2007)              |
| Salt            | Tomato ( <i>Lycopersicon esculentum</i> ) | <i>Achromobacter piechaudii</i>   | (Mayak et al., 2004a)              |
| Salt            | Wheat ( <i>Triticum aestivum</i> )        | <i>Aeromonas hydrophila/caviae</i>  | (Ashraf et al., 2004)              |
| Salt            | Groundnut ( <i>Arachis hypogaea</i> )     | <i>Enterobacter aerogenes</i><br><i>Pseudomonas fluorescens</i>                                   | (Saravanakumar & Samiyappan, 2007) |
| Salt            | Lettuce ( <i>Lactuca sativa</i> )         | <i>Azospirillum sp.</i>   | (Barassi et al., 2006)             |
| Salt            | Maize ( <i>Zea mays</i> )                 | <i>Azospirillum</i>   | (Hamdia et al., 2004)              |
| Salt            | Chickpeas ( <i>Cicer arietinum</i> )      | <i>Azospirillum brasilense</i>  | (Hamaoui et al., 2001)             |
| Drying soil     | Pea ( <i>Pisum sativum</i> )              | <i>Variovorax paradoxus</i>   | (Wang et al., 2016)                |
| Drying soil     | Lettuce ( <i>Lactuca sativa</i> )         | <i>Bacillus sp.</i>   | (Arkhipova et al., 2007)           |
| Drought         | Tomato ( <i>Lycopersicon esculentum</i> ) | <i>Achromobacter piechaudii</i>   | (Mayak et al., 2004b)              |
| Drought         | Wheat ( <i>Triticum aestivum</i> )        | <i>Azospirillum sp.</i>   | (Creus et al., 2004)               |
| Temperature     | Grapevine ( <i>Vitis vinifera</i> )       | <i>Burkholderia phytofirmans</i>  | (Ait Barka et al., 2006)           |
| Temperature     | Soybean ( <i>Glycine max</i> )            | <i>Aeromonas hydrophila</i> ,<br><i>Serratia liquefaciens</i> ,<br><i>Serratia proteamaculans</i> | (Zhang et al., 1997)               |
| Iron toxicity   | Rice ( <i>Oryza sativa</i> )              | <i>Bacillus subtilis</i> , <i>Bacillus megaterium</i> ,   | (Asch & Padham, 2005)              |

## **Future Prospects-**

With constantly worsening environmental conditions and an increasing dependence on agricultural output, phosphate unavailability and the impact of various biotic and abiotic stressors is posing an increasing threat to our reliance on crops. PSBs and PGPRs have already demonstrated a mitigating effect in both maintaining phosphate availability and tackling the various stress factors. However, more focus needs to be placed on understanding the working mechanism of various PSBs against such stressors at a molecular level. Isolation and characterization of PSB from soil which is facing these stress factors such as hypersaline soil, drought-afflicted soil and alkaline soils is pertinent in understanding the underlying pathways through which protection is offered. Therefore, it is necessary to perform thorough and detailed research on PSBs in order to effectively utilize them for maintaining our agricultural output even in the scarcity of available phosphorous and in the presence of various stressors.

## **Conclusion-**

Due to anthropogenic activity and natural, climate change, there are more abiotic and biotic pressures influencing the world's primary crop output. The most significant abiotic stress conditions, such as low/high temperature, drought and salinity, which result in substantial agricultural yield stagnation and economic losses, also have an impact on beneficial soil-plant microorganisms. On the other hand, the ability of soil microbes to cause plant responses to stress factors through mechanisms including induced systemic tolerance has increased their importance in fostering plant development and improving overall plant health. Therefore, one of the most significant challenges is the development of biotechnological strategies for the management of micro-organisms associated with plants. The ability of phosphate solubilizing microorganisms to tolerate abiotic stress factors while maintaining their solubilizing potential has been demonstrated by a large body of evidence in recent years.

It has been demonstrated in multiple studies that PSBs have the ability to alleviate a wide range of abiotic stresses including drought and salt stress. Two major environmental stresses are drought and extreme environmental temperatures, both of which cause plant stress such as osmotic and oxidative stress that affect plant physiology and biochemistry leading to plant death or significant loss in crop productivity. For farmers, salt stress remains a serious issue. It wreaks havoc on the soil, plant development, and crop yields. The mechanisms used by plants to handle this stress are unique. Phosphate chemical fertiliser use has detrimental

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effects on environmental problems. An alternative strategy in this situation would be to apply phosphate biofertilizers like PSB, which can improve nutrient uptake, creating plant growth hormones and serve as a biocontrol agent. These bacteria develop phosphorous management strategy that is both affordable and effective. Their potential applications as a alternative of chemical fertilizers and their simultaneous protective action against various environmental stressors highlight them as an important commodity in the agricultural sector for increasing the global crop output.

## References-

- Abdul Rahman, N. S. N., Abdul Hamid, N. W., & Nadarajah, K. (2021). Effects of Abiotic Stress on Soil Microbiome. *International Journal of Molecular Sciences*, 22(16), 9036. <https://doi.org/10.3390/ijms22169036>
- Ahanger, M. A., Hashem, A., Abd-Allah, E. F., & Ahmad, P. (2014). Chapter 3—Arbuscular Mycorrhiza in Crop Improvement under Environmental Stress. In P. Ahmad & S. Rasool (Eds.), *Emerging Technologies and Management of Crop Stress Tolerance* (pp. 69–95). Academic Press. <https://doi.org/10.1016/B978-0-12-800875-1.00003-X>
- Ait Barka, E., Nowak, J., & Clément, C. (2006). Enhancement of Chilling Resistance of Inoculated Grapevine Plantlets with a Plant Growth-Promoting Rhizobacterium, Burkholderia phytofirmans Strain PsJN. *Applied and Environmental Microbiology*, 72(11), 7246–7252. <https://doi.org/10.1128/AEM.01047-06>
- Al-Busaidi, A., Ahmed, M., & Chikara, J. (2012). The impact of heat and water stress conditions on the growth of the biofuel plant *Jatropha curcas*. *International Journal of Environmental Studies*, 69(2), 273–288. <https://doi.org/10.1080/00207233.2012.663204>
- Alexandre, A., & Oliveira, S. (2011). Most heat-tolerant rhizobia show high induction of major chaperone genes upon stress: High induction of dnaK and groESL in heat-tolerant rhizobia. *FEMS Microbiology Ecology*, 75(1), 28–36. <https://doi.org/10.1111/j.1574-6941.2010.00993.x>
- Arkhipova, T. N., Prinsen, E., Veselov, S. U., Martinenko, E. V., Melentiev, A. I., & Kudoyarova, G. R. (2007). Cytokinin producing bacteria enhance plant growth in drying soil. *Plant and Soil*, 292(1), 305–315. <https://doi.org/10.1007/s11104-007-9233-5>
- Artiola, J. F., Walworth, J. L., Musil, S. A., & Crimmins, M. A. (2019). Chapter 14—Soil and Land Pollution. In M. L. Brusseau, I. L. Pepper, & C. P. Gerba (Eds.), *Environmental and Pollution Science (Third Edition)* (pp. 219–235). Academic Press. <https://doi.org/10.1016/B978-0-12-814719-1.00014-8>
- Arzanesh, M. H., Alikhani, H. A., Khavazi, K., Rahimian, H. A., & Miransari, M. (2011). Wheat (*Triticum aestivum* L.) growth enhancement by *Azospirillum* sp. Under drought stress. *World Journal of Microbiology and Biotechnology*, 27(2), 197–205. <https://doi.org/10.1007/s11274-010-0444-1>
- Asch, F., & Padham, J. L. (2005). Root associated bacteria suppress symptoms of iron toxicity in lowland rice. *The Global Food & Product Chain—Dynamics, Innovations, Conflicts, Strategies*. MDD GmbH, Stuttgart, 276.
- Ashraf, M., Hasnain, S., Berge, O., & Mahmood, T. (2004). Inoculating wheat seedlings with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. *Biology and Fertility of Soils*, 40(3), 157–162. <https://doi.org/10.1007/s00374-004-0766-y>
- Azzi, V., Kanso, A., Kazpard, V., Kobeissi, A., Lartiges, B., & El Samrani, A. (2017). *Lactuca sativa* growth in compacted and non-compacted semi-arid alkaline soil under



phosphate fertilizer treatment and cadmium contamination. *Soil and Tillage Research*, 165, 1–10. <https://doi.org/10.1016/j.still.2016.07.014>

Barassi, C. A., Ayrault, G., Creus, C. M., Sueldo, R. J., & Sobrero, M. T. (2006). Seed inoculation with *Azospirillum* mitigates NaCl effects on lettuce. *Scientia Horticulturae*, 109(1), 8–14. <https://doi.org/10.1016/j.scienta.2006.02.025>

Ben Ahmed, C., Ben Rouina, B., Sensoy, S., Boukhriss, M., & Ben Abdullah, F. (2010). Exogenous Proline Effects on Photosynthetic Performance and Antioxidant Defense System of Young Olive Tree. *Journal of Agricultural and Food Chemistry*, 58(7), 4216–4222. <https://doi.org/10.1021/jf9041479>

Bouzigaren, A., Farissi, M., Ghoulam, C., Kallida, R., Faghire, M., Barakate, M., & Al Feddy, M. N. (2013). Assessment of summer drought tolerance variability in Mediterranean alfalfa (*Medicago sativa* L.) cultivars under Moroccan fields conditions. *Archives of Agronomy and Soil Science*, 59(1), 147–160. <https://doi.org/10.1080/03650340.2011.606216>

Chang Lee, C., Huang, H. T., Wu, Y. C., Kao, Y. T., & Chen, H. L. (2018). The Health Risks of Lead and Cadmium in Foodstuffs for the General Population of Taiwan. *Journal of Experimental Food Chemistry*, 04(01). <https://doi.org/10.4172/2472-0542.1000137>

Corpas, F. J., Leterrier, M., Valderrama, R., Airaki, M., Chaki, M., Palma, J. M., & Barroso, J. B. (2011). Nitric oxide imbalance provokes a nitrosative response in plants under abiotic stress. *Plant Science*, 181(5), 604–611. <https://doi.org/10.1016/j.plantsci.2011.04.005>

Creus, C. M., Sueldo, R. J., & Barassi, C. A. (2004). Water relations and yield in *Azospirillum*-inoculated wheat exposed to drought in the field. *Canadian Journal of Botany*, 82(2), 273–281.

Dardanelli, M. S., Fernández de Córdoba, F. J., Espuny, M. R., Rodríguez Carvajal, M. A., Soria Díaz, M. E., Gil Serrano, A. M., Okon, Y., & Megías, M. (2008). Effect of *Azospirillum brasilense* coinoculated with *Rhizobium* on *Phaseolus vulgaris* flavonoids and Nod factor production under salt stress. *Soil Biology and Biochemistry*, 40(11), 2713–2721. <https://doi.org/10.1016/j.soilbio.2008.06.016>

Das, K., Katiyar, V., & Goel, R. (2003). ‘P’ solubilization potential of plant growth promoting *Pseudomonas* mutants at low temperature. *Microbiological Research*, 158(4), 359–362. <https://doi.org/10.1078/0944-5013-00217>

Dash, B., Soni, R., & Goel, R. (2019). Rhizobacteria for Reducing Heavy Metal Stress in Plant and Soil. In R. Z. Sayyed, N. K. Arora, & M. S. Reddy (Eds.), *Plant Growth Promoting Rhizobacteria for Sustainable Stress Management: Volume 1: Rhizobacteria in Abiotic Stress Management* (pp. 179–203). Springer. [https://doi.org/10.1007/978-981-13-6536-2\\_10](https://doi.org/10.1007/978-981-13-6536-2_10)

Dey, G., Banerjee, P., Sharma, R. K., Maity, J. P., Etesami, H., Shaw, A. K., Huang, Y.-H., Huang, H.-B., & Chen, C.-Y. (2021). Management of Phosphorus in Salinity-Stressed Agriculture for Sustainable Crop Production by Salt-Tolerant Phosphate-Solubilizing Bacteria—A Review. *Agronomy*, 11(8), Article 8. <https://doi.org/10.3390/agronomy11081552>

Dimkpa, C., Weinand, T., & Asch, F. (2009). Plant–rhizobacteria interactions alleviate abiotic stress conditions. *Plant, Cell & Environment*, *32*(12), 1682–1694. <https://doi.org/10.1111/j.1365-3040.2009.02028.x>

Ding, Z., Kheir, A. M. S., Ali, M. G. M., Ali, O. A. M., Abdelaal, A. I. N., Lin, X., Zhou, Z., Wang, B., Liu, B., & He, Z. (2020). The integrated effect of salinity, organic amendments, phosphorus fertilizers, and deficit irrigation on soil properties, phosphorus fractionation and wheat productivity. *Scientific Reports*, *10*(1), 2736. <https://doi.org/10.1038/s41598-020-59650-8>

Đukić, D., & Mandić, L. (2006). Microorganisms as indicators of soil pollution with heavy metals. *Acta Agriculturae Serbica*, *11*(22), 45–55.

Garg, V. K., Yadav, P., Mor, S., Singh, B., & Pulhani, V. (2014). Heavy Metals Bioconcentration from Soil to Vegetables and Assessment of Health Risk Caused by Their Ingestion. *Biological Trace Element Research*, *157*(3), 256–265. <https://doi.org/10.1007/s12011-014-9892-z>

Greer, D. H., & Weedon, M. M. (2012). Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate. *Plant, Cell & Environment*, *35*(6), 1050–1064. <https://doi.org/10.1111/j.1365-3040.2011.02471.x>

Groß, F., Durner, J., & Gaupels, F. (2013). Nitric oxide, antioxidants and prooxidants in plant defence responses. *Frontiers in Plant Science*, *4*. <https://www.frontiersin.org/articles/10.3389/fpls.2013.00419>

Gulati, A., Vyas, P., Rahi, P., & Kasana, R. C. (2009). Plant Growth-Promoting and Rhizosphere-Competent *Acinetobacter rhizosphaerae* Strain BIHB 723 from the Cold Deserts of the Himalayas. *Current Microbiology*, *58*(4), 371–377. <https://doi.org/10.1007/s00284-008-9339-x>

Hamaoui, B., Abbadi, J., Burdman, S., Rashid, A., Sarig, S., & Okon, Y. (2001). Effects of inoculation with *Azospirillum brasilense* on chickpeas (*Cicer arietinum*) and faba beans (*Vicia faba*) under different growth conditions. *Agronomie*, *21*(6–7), 553–560.

Hamdia, M. A. E.-S., Shaddad, M. A. K., & Doaa, M. M. (2004). Mechanisms of salt tolerance and interactive effects of *Azospirillum brasilense* inoculation on maize cultivars grown under salt stress conditions. *Plant Growth Regulation*, *44*, 165–174.

Hartmann, M., & Six, J. (2023). Soil structure and microbiome functions in agroecosystems. *Nature Reviews Earth & Environment*, *4*(1), Article 1. <https://doi.org/10.1038/s43017-022-00366-w>

Hidayat, I. (2019). Dark Septate Endophytes and Their Role in Enhancing Plant Resistance to Abiotic and Biotic Stresses. In R. Z. Sayyed, N. K. Arora, & M. S. Reddy (Eds.), *Plant Growth Promoting Rhizobacteria for Sustainable Stress Management: Volume 1: Rhizobacteria in Abiotic Stress Management* (pp. 35–63). Springer. [https://doi.org/10.1007/978-981-13-6536-2\\_3](https://doi.org/10.1007/978-981-13-6536-2_3)

Huang, J., Xu, C., Ridoutt, B. G., Wang, X., & Ren, P. (2017). Nitrogen and phosphorus losses and eutrophication potential associated with fertilizer application to cropland in China. *Journal of Cleaner Production*, *159*, 171–179. <https://doi.org/10.1016/j.jclepro.2017.05.008>

- Kang, S.-M., Khan, M.-A., Hamayun, M., Kim, L.-R., Kwon, E.-H., Kang, Y.-S., Kim, K.-Y., Park, J.-J., & Lee, I.-J. (2021). Phosphate-Solubilizing Enterobacter ludwigii AFFR02 and Bacillus megaterium Mj1212 Rescues Alfalfa's Growth under Post-Drought Stress. *Agriculture*, 11(6), Article 6. <https://doi.org/10.3390/agriculture11060485>
- Kim, Y. S., Lee, M., Lee, J.-H., Lee, H.-J., & Park, C.-M. (2015). The unified ICE–CBF pathway provides a transcriptional feedback control of freezing tolerance during cold acclimation in Arabidopsis. *Plant Molecular Biology*, 89(1), 187–201. <https://doi.org/10.1007/s11103-015-0365-3>
- Kour, D., Rana, K. L., Kaur, T., Yadav, N., Yadav, A. N., Kumar, M., Kumar, V., Dhaliwal, H. S., & Saxena, A. K. (2021). Biodiversity, current developments and potential biotechnological applications of phosphorus-solubilizing and -mobilizing microbes: A review. *Pedosphere*, 31(1), 43–75. [https://doi.org/10.1016/S1002-0160\(20\)60057-1](https://doi.org/10.1016/S1002-0160(20)60057-1)
- Kour, D., Rana, K. L., Yadav, A. N., Sheikh, I., Kumar, V., Dhaliwal, H. S., & Saxena, A. K. (2020). Amelioration of drought stress in Foxtail millet (*Setaria italica* L.) by P-solubilizing drought-tolerant microbes with multifarious plant growth promoting attributes. *Environmental Sustainability*, 3(1), 23–34. <https://doi.org/10.1007/s42398-020-00094-1>
- Machado, R. M. A., & Serralheiro, R. P. (2017). Soil Salinity: Effect on Vegetable Crop Growth. Management Practices to Prevent and Mitigate Soil Salinization. *Horticulturae*, 3(2), Article 2. <https://doi.org/10.3390/horticulturae3020030>
- Martinez, V., Nieves-Cordones, M., Lopez-Delacalle, M., Rodenas, R., Mestre, T. C., Garcia-Sanchez, F., Rubio, F., Nortes, P. A., Mittler, R., & Rivero, R. M. (2018). Tolerance to Stress Combination in Tomato Plants: New Insights in the Protective Role of Melatonin. *Molecules*, 23(3), Article 3. <https://doi.org/10.3390/molecules23030535>
- Mayak, S., Tirosh, T., & Glick, B. R. (2004a). Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. *Plant Physiology and Biochemistry*, 42(6), 565–572. <https://doi.org/10.1016/j.plaphy.2004.05.009>
- Mayak, S., Tirosh, T., & Glick, B. R. (2004b). Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. *Plant Science*, 166(2), 525–530.
- Mohammed, A. S., Kapri, A., & Goel, R. (2011). Heavy metal pollution: Source, impact, and remedies. *Bio-management of Metal-Contaminated Soils*, 1–28.
- Mohan, V., Devi K, S., Anushya, A., Revathy, G., Kuzhalvaimozhi, G., & Vijayalakshmi, K. (2017). *Screening of Salt Tolerant and Growth Promotion Efficacy of Phosphate Solubilizing Bacteria*. 5.
- Nadeem, S. M., Zahir, Z. A., Naveed, M., & Arshad, M. (2007). Preliminary investigations on inducing salt tolerance in maize through inoculation with rhizobacteria containing ACC deaminase activity. *Canadian Journal of Microbiology*, 53(10), 1141–1149. <https://doi.org/10.1139/W07-081>
- Nautiyal, C. S., Bhadauria, S., Kumar, P., Lal, H., Mondal, R., & Verma, D. (2000). Stress induced phosphate solubilization in bacteria isolated from alkaline soils. *FEMS Microbiology Letters*, 182(2), 291–296. <https://doi.org/10.1111/j.1574-6968.2000.tb08910.x>

- Numan, M., Bashir, S., Khan, Y., Mumtaz, R., Shinwari, Z. K., Khan, A. L., Khan, A., & AL-Harrasi, A. (2018). Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: A review. *Microbiological Research*, 209, 21–32. <https://doi.org/10.1016/j.micres.2018.02.003>
- Olanrewaju, O. S., Glick, B. R., & Babalola, O. O. (2017). Mechanisms of action of plant growth promoting bacteria. *World Journal of Microbiology and Biotechnology*, 33(11), 197. <https://doi.org/10.1007/s11274-017-2364-9>
- Osakabe, Y., Osakabe, K., Shinozaki, K., & Tran, L.-S. (2014). Response of plants to water stress. *Frontiers in Plant Science*, 5. <https://www.frontiersin.org/articles/10.3389/fpls.2014.00086>
- Padmavathi, T. (2015). Optimization of phosphate solubilization by aspergillus niger using plackett-burman and response surface methodology. *Journal of Soil Science and Plant Nutrition, ahead*, 0–0. <https://doi.org/10.4067/S0718-95162015005000053>
- Pandey, S., & Gupta, S. (2020). Diversity analysis of ACC deaminase producing bacteria associated with rhizosphere of coconut tree (*Cocos nucifera* L.) grown in Lakshadweep islands of India and their ability to promote plant growth under saline conditions. *Journal of Biotechnology*, 324, 183–197. <https://doi.org/10.1016/j.jbiotec.2020.10.024>
- Riadh, K., Wided, M., Hans-Werner, K., & Chedly, A. (2010). Responses of Halophytes to Environmental Stresses with Special Emphasis to Salinity. In J.-C. Kader & M. Delseny (Eds.), *Advances in Botanical Research* (Vol. 53, pp. 117–145). Academic Press. [https://doi.org/10.1016/S0065-2296\(10\)53004-0](https://doi.org/10.1016/S0065-2296(10)53004-0)
- Ruan, C.-J., da Silva, J. A. T., Mopper, S., Qin, P., & Lutts, S. (2010). Halophyte Improvement for a Salinized World. *Critical Reviews in Plant Sciences*, 29(6), 329–359. <https://doi.org/10.1080/07352689.2010.524517>
- Saeed, Q., Xiukang, W., Haider, F. U., Kučerik, J., Mumtaz, M. Z., Holatko, J., Naseem, M., Kintl, A., Ejaz, M., Naveed, M., Brtnicky, M., & Mustafa, A. (2021). Rhizosphere Bacteria in Plant Growth Promotion, Biocontrol, and Bioremediation of Contaminated Sites: A Comprehensive Review of Effects and Mechanisms. *International Journal of Molecular Sciences*, 22(19), 10529. <https://doi.org/10.3390/ijms221910529>
- Sahu, P., Gupta, A., Sharma, L., & Bakade, R. (2017). *Mechanisms of Azospirillum in Plant Growth Promotion*. <https://www.semanticscholar.org/paper/Mechanisms-of-Azospirillum-in-Plant-Growth-Sahu-Gupta/2ea82f4a4da866f71e78bdd993d6ad8abc4934>
- Salim, A., Cheloufi, H., Attab, S., & Bouras, N. (2019). IMPROVEMENT OF ALFALFA GROWTH UNDER WATER STRESS BY INOCULATION WITH SINORHIZOBIUM MELILOTI STRAINS FROM THE ALGERIAN SAHARA. *PONTE International Scientific Researchs Journal*, 75. <https://doi.org/10.21506/j.ponte.2019.7.4>
- Saluja, B., & Sharma, V. (2014). Cadmium Resistance Mechanism in Acidophilic and Alkalophilic Bacterial Isolates and their Application in Bioremediation of Metal-Contaminated Soil. *Soil and Sediment Contamination: An International Journal*, 23(1), 1–17. <https://doi.org/10.1080/15320383.2013.772094>

Sandhya, V., Ali, Sk. Z., Grover, M., Reddy, G., & Venkateswarlu, B. (2010). Effect of plant growth promoting *Pseudomonas* spp. On compatible solutes, antioxidant status and plant growth of maize under drought stress. *Plant Growth Regulation*, 62(1), 21–30. <https://doi.org/10.1007/s10725-010-9479-4>

Saravanakumar, D., & Samiyappan, R. (2007). ACC deaminase from *Pseudomonas fluorescens* mediated saline resistance in groundnut (*Arachis hypogea*) plants. *Journal of Applied Microbiology*, 102(5), 1283–1292. <https://doi.org/10.1111/j.1365-2672.2006.03179.x>

Saxena, S. C., Kaur, H., Verma, P., Petla, B. P., Andugula, V. R., & Majee, M. (2013). Osmoprotectants: Potential for Crop Improvement Under Adverse Conditions. In N. Tuteja & S. Singh Gill (Eds.), *Plant Acclimation to Environmental Stress* (pp. 197–232). Springer. [https://doi.org/10.1007/978-1-4614-5001-6\\_9](https://doi.org/10.1007/978-1-4614-5001-6_9)

Scharf, K.-D., Berberich, T., Ebersberger, I., & Nover, L. (2012). The plant heat stress transcription factor (Hsf) family: Structure, function and evolution. *Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms*, 1819(2), 104–119. <https://doi.org/10.1016/j.bbagr.2011.10.002>

Sharan, A., Shikha, Darmwal, N. S., & Gaur, R. (2008). *Xanthomonas campestris*, a novel stress tolerant, phosphate-solubilizing bacterial strain from saline–alkali soils. *World Journal of Microbiology and Biotechnology*, 24(6), 753–759. <https://doi.org/10.1007/s11274-007-9535-z>

Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., & Gobi, T. A. (2013). Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *SpringerPlus*, 2, 1–14.

Sobariu, D. L., Fertu, D. I. T., Diaconu, M., Pavel, L. V., Hlihor, R.-M., Drăgoi, E. N., Curteanu, S., Lenz, M., Corvini, P. F.-X., & Gavrilescu, M. (2017). Rhizobacteria and plant symbiosis in heavy metal uptake and its implications for soil bioremediation. *New Biotechnology*, 39, 125–134. <https://doi.org/10.1016/j.nbt.2016.09.002>

Sundseth, K., Pacyna, J. M., Pacyna, E. G., Pirrone, N., & Thorne, R. J. (2017). Global Sources and Pathways of Mercury in the Context of Human Health. *International Journal of Environmental Research and Public Health*, 14(1), Article 1. <https://doi.org/10.3390/ijerph14010105>

Tan, W., Meng, Q. wei, Brestic, M., Olsovska, K., & Yang, X. (2011). Photosynthesis is improved by exogenous calcium in heat-stressed tobacco plants. *Journal of Plant Physiology*, 168(17), 2063–2071. <https://doi.org/10.1016/j.jplph.2011.06.009>

Tchounwou, P. B., Yedjou, C. G., Patlolla, A. K., & Sutton, D. J. (2012). Heavy Metals Toxicity and the Environment. *EXS*, 101, 133–164. [https://doi.org/10.1007/978-3-7643-8340-4\\_6](https://doi.org/10.1007/978-3-7643-8340-4_6)

Titah, H. S., Siti Rozaimah, S. A., Mushrifah, I., Anuar, N., Basri, H., & Mukhlisin, M. (2014). Identification of rhizobacteria from *Ludwigia octovalvis* grown in arsenic. *Australian Journal of Basic and Applied Sciences*, 8(Special 3), 134–139.

Vassilev, N., Eichler-Löbermann, B., & Vassileva, M. (2012). Stress-tolerant P-solubilizing microorganisms. *Applied Microbiology and Biotechnology*, 95(4), 851–859. <https://doi.org/10.1007/s00253-012-4224-8>

Vijayadeep, S. (2014). Effect of Heavy Metal Uptake by *E. coli* and *Bacillus* sps. *Journal of Bioremediation & Biodegradation*, 05(05). <https://doi.org/10.4172/2155-6199.1000238>

Wani, A. L., Ara, A., & Usmani, J. A. (2015). Lead toxicity: A review. *Interdisciplinary Toxicology*, 8(2), 55–64. <https://doi.org/10.1515/intox-2015-0009>

Xu, R., Li, T., Cui, H., Wang, J., Yu, X., Ding, Y., Wang, C., Yang, Z., & Zhao, Z. (2015). Diversity and characterization of Cd-tolerant dark septate endophytes (DSEs) associated with the roots of Nepal alder (*Alnus nepalensis*) in a metal mine tailing of southwest China. *Applied Soil Ecology*, 93, 11–18. <https://doi.org/10.1016/j.apsoil.2015.03.013>

Yadav. (2022). Phosphate-Solubilizing Microorganisms for Agricultural Sustainability. *Journal of Applied Biology & Biotechnology*, 1–6. <https://doi.org/10.7324/JABB.2022.103ed>

Yadav, P., Singh, B., Garg, V. K., Mor, S., & Pulhani, V. (2017). Bioaccumulation and health risks of heavy metals associated with consumption of rice grains from croplands in Northern India. *Human and Ecological Risk Assessment: An International Journal*, 23(1), 14–27. <https://doi.org/10.1080/10807039.2016.1218750>

Yarzabal, L. A. (2014). Cold-Tolerant Phosphate-Solubilizing Microorganisms and Agriculture Development in Mountainous Regions of the World. In M. S. Khan, A. Zaidi, & J. Musarrat (Eds.), *Phosphate Solubilizing Microorganisms: Principles and Application of Microphos Technology* (pp. 113–135). Springer International Publishing. [https://doi.org/10.1007/978-3-319-08216-5\\_5](https://doi.org/10.1007/978-3-319-08216-5_5)

Yeo, B., & Langley-Turnbaugh, S. (2010). Trace Element Deposition on Mount Everest. *Soil Survey Horizons*, 51(3), 72–78. <https://doi.org/10.2136/sh2010.3.0072>

Zhang, F., Dashti, N., Hynes, R. K., & Smith, D. L. (1997). Plant growth-promoting rhizobacteria and soybean [*Glycine max* (L.) Merr.] growth and physiology at suboptimal root zone temperatures. *Annals of Botany*, 79(3), 243–249.

Zhang, X., St. Leger, R. J., & Fang, W. (2017). Pyruvate Accumulation Is the First Line of Cell Defense against Heat Stress in a Fungus. *MBio*, 8(5), e01284-17. <https://doi.org/10.1128/mBio.01284-17>