The Pharma Innovation Journal 2024; 13(3): 326-339

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The Pharma Innovation

How does abiotic stress influence on plant microbe interactions: A review

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ISSN (E): 2277-7695
ISSN (P): 2349-8242
TPI 2024; 13(3): 326-339

www.thepharmajournal.com
Received: 17-12-2023
Accepted: 29-01-2024

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Abstract

Abiotic stress is a critical limiting factor for crop output, food quality, and global food security. Plant physiological, biochemical, and molecular characteristics are all impacted when they are stressed. The loss of soil microbial diversity, soil fertility, and competition for nutrient resources are the main effects of these pressures. Because the use of inorganic fertilizers and pesticides in agriculture techniques depletes soil fertility and pollutes the ecosystem. As a result, it is vital to develop more secure and long-term agricultural production methods. Plant growth promoting microorganisms (PGPM) and mycorrhizal fungi are used to improve plant development. It provides a cost-effective and environmentally friendly means of shielding plants from stress. Plant growth may be aided by PGPM, which regulates plant hormones, improves nutrient acquisition, produces siderophores, and boosts the antioxidant system. Arbuscular mycorrhizae (AM) boost stress tolerance by increasing the delivery of nutrients and water during stressful situations. Because it relies on biological processes and replaces conventional agriculture procedures, this plant-microbe interaction is critical for sustainable agriculture and industrial purposes. As a result, bacteria may play an important role as an ecological engineer in resolving environmental issues.

Keywords: Abiotic stress, plant-microbe interaction, mycorrhizal fungi, plant growth promoting microbes (PGPM)

1. Introduction

The twenty-first century has seen global climate change. Despite the fact that the world's population is predicted to expand from 7 billion people today to 8.9 billion by 2050 (Battisti and Naylor,2009) [32], many research studies have indicated that environmental factors pose a severe global threat to future food security. (Singh *et al.* 2011) [3] Climate variability, population growth, and worsening soil health for crop production are all threatening agricultural sustainability. It may become more widespread in the future due to climate change and vast farming techniques (Wassmann *et al.*, 2009) [34]. It may become more widespread in the future as a result of climate change and vast farming operations (Wassmann *et al.*, 2009) [34]. Farmers and policymakers are finding it increasingly challenging to produce enough food to meet the demands of a growing population as our existing agriculture population grows (Masciarelli *et al.*, 2014) [35]. Chemical fertilizers, insecticides, weedicides, and other agricultural chemicals applied indiscriminately, on the other hand, result in a large loss of beneficial microbial diversity in the soil. Our agro-ecosystem is always under biotic and abiotic stress, influencing production and yield. Various stress factors have a negative impact on crop plant growth and yield. Abiotic and biotic stress are the two types of stress. Abiotic and biotic stress are responsible for 50% and 30% of global agricultural productivity losses, respectively. Abiotic and biotic stress can be natural or produced by humans. Temperature, dryness, salinity, and heavy metal stress are the most significant abiotic stressors. The impacts of stress on plant morphology, physiology, biochemistry, and even gene regulation are numerous. In relation to climate change, temperature, water scarcity, salinity, and heavy metal pollution are all key stressors. Abiotic stress variables also have an impact on biotic stress, lowering crop output. The loss of soil microbial diversity, soil fertility, and competition for nutrient resources are the main effects of these pressures (Chodak *et al.*, 2015) [36]. Plant-associated microbial communities, such as mycorrhizal fungi and plant growth promoting bacteria (PGPB), are the only viable alternatives, as they aid plant growth and development under a variety of abiotic and biotic conditions. Plant growth promoting rhizobacteria (PGPR) and mycorrhizal fungi are examples of effective microorganisms that can aid with sustainable agriculture and environmental stability.

Microbes linked with plants are divided into three categories based on their effects on plants: helpful, harmful, and neutral. PGPR refers to a group of bacteria including Pseudomonas, Enterobacter, *Bacillus*, Variovorax, Klebsiella, Burkholderia, Azospirillum, Serratia, and *Azotobacter* that support plant growth and development in both normal and stressful conditions. Drought, salt, and heavy metal stress are all too much for most plant growth promoting microorganisms (PGPM) and arbuscular mycorrhizae (AM).

2. Brief overview of abiotic stresses and secondary stresses

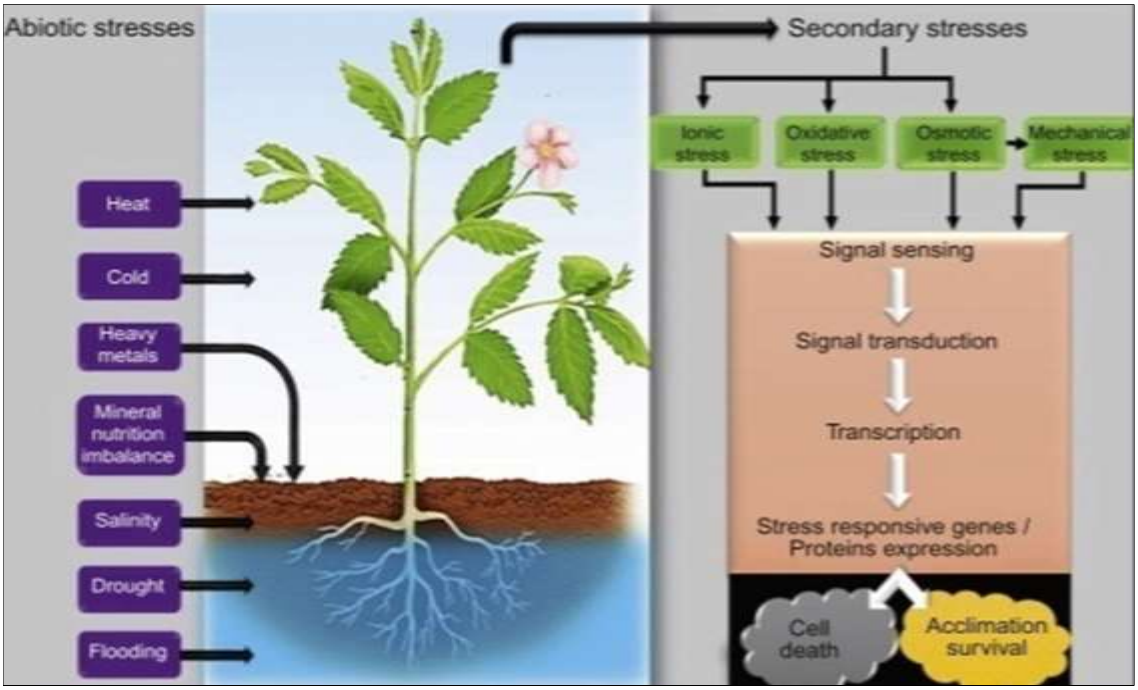


Fig 1: Diagrammatic representation of mechanism of Salinity stresses tolerance

2.1 Plant–microbe interactions: PGPM assisting stress tolerance

The application of stress-tolerant PGPM and AM fungus to plants may help them develop and survive under difficult situations (Nadeem *et al.*,2014) [39]. Microbes used both indirect and direct processes to help plants grow and develop amid stressful situations. Microbes boost their growth and development through many biochemical and molecular pathways. Inoculation with PGPM, for example, promotes plant development by controlling hormonal and nutritional balance, generating plant growth regulator, and imparting resistance to phytopathogens (Spence and Bais, 2015) [40]. PGPM produce certain metabolites which reduced pathogen population around plant surrounding. For example, Siderophore produced by these microbes in rhizosphere reduced iron availability to certain pathogens and resultedin reduced their growth (Złoch *et al.*, 2016) [41]. They also help plants grow by fixing nitrogen from the air, solubilizing phosphate, and generating plant hormones (Ahmad *et al.*, 2011) [4]. Other strategies that help the plant adapt with the unfavourable environment include nutrient mobilisation, exopolysaccharide formation, rhizobitoxine production, and so on (Vardharajula *et al.*, 2011) [17]. Rhizobitoxine inhibits the production of ethylene, which helps plants grow and develop in stressful situations (Kumar *et al.*, 2009) [43]. In addition, important enzymes such as ACC-deaminase, chitinase, and glucanase may have the ability to improve plant growth and development under stress conditions (Farooq *et al.*, 2009) [42]. Furthermore, some bacteria have sigma factors that allow them to modify gene expression in unfavourable conditions in order to counteract detrimental effects (Gupta *et al.*, 2013) [44]. Aside from PGPM, another crucial aspect of growth and development is the interaction of fungi with the root of the higher plant. AM is the most frequent type of mycorrhizae found in agricultural fields. These fungi play a crucial role in nutrient cycle, absorption, and translocation. These microbial processes assist the plant in maintaining its current growth in a stressful environment by reducing the detrimental effects of stress on plant growth and development. As a result, the PGPM were discovered to be a viable alternative to inorganic fertilisers and insecticides.

2.1.1 Mechanism of drought stress tolerance

Drought-tolerant microorganisms have the potential to improve plant growth and development when there is a lack of water. Microbes have evolved, adapted, and/or developed a tolerance mechanism to enable them to exist in low water potential environments (Table 1). They can gather osmolytes and create exopolysaccharides, and they can develop thick walls or go inactive (EPS). These plant-associated microorganisms use a variety of ways to counteract the harmful effects of drought on both plants and soil. They give fertiliser and better environmental conditions for plant growth regardless of water content. Plant growth and development are aided by the beneficial microorganisms that populate the rhizosphere through a variety of direct and indirect methods. (1) synthesis of phytohormones such indole-3-acetic acid (IAA), cytokinins, and abscisic acid (ABA) (2) bacterial exopolysaccharides (3) ACC deaminase (4) increased systemic tolerance are all possible mechanisms. Plant-produced phytohormones play an important role in growth and development (Farooq *et al.*, 2009; Porcel *et al.*, 2014) [42, 88]. PGPR also has the ability to generate plant hormones that promote plant growth and division in stressful situations. During drought stress, IAA, a highly active auxin, governs vascular tissue differentiation, adventitious and lateral root differentiation, cell division, and shoot growth (Goswami *et al*., 2015) [46]. During drought stress, the ABA plays a crucial role as a growth regulator. It has been reported that When a seed or plant is injected with PGPR, the concentration of ABA rises, regulating plant physiology to withstand drought. Drought stress is alleviated by ABA through modulating drought-related gene transcription and root hydraulic conductivity (Jiang *et al*., 2013) [47]. Azospirillum brasilense, for example, improves Arabidopsis thaliana's drought response mostly through increasing ABA levels (Cohen *et al*., 2015) [48]. (Table 1). During times of stress, 1-aminocyclopropane-1-carboxylate (ACC) is an immediate precursor of ethylene. ACC is hydrolyzed by bacterial ACC deaminase into ammonia and alphaketobutyrate (Bal *et al*., 2013) [11, 27]. Drought stress tolerance and PGPR improve biomass, water potential, and decrease water loss in stressed maize plants. These inoculants reduce antioxidant activity while increasing proline, free amino acid, and sugar synthesis in plants (Vardharajula *et al*., 2011) [17]. The amount of chlorophyll in the soybean plant diminishes when there is a lack of water, which affects photosynthesis. To counteract this impact, inoculation with *Pseudomonas putida* H-2-3 is required, which reduces drought stress by increasing chlorophyll content, increasing shoot length, and increasing biomass (Kang *et al*.,2014) [89]. Furthermore, combining endophytic and rhizosphere PGPR improves stress tolerance. Microbe-produced exopolysaccharide improves drought tolerance in some plants. Three drought-tolerant bacterial strains, Proteus penneri (Pp1), Pseudomonas aeruginosa (Pa2), and *Alcaligenes faecalis* (AF3), were inoculated with a maize plant and exhibited potential increases in relative water content, protein, and sugar, however the proline level was higher (Naseem and Bano 2014) [90]. In order to survive in such a drought, To protect themselves from harmful conditions, bacteria develop a number of physiological, biochemical, and molecular mechanisms. They produce EPS, a compatible solute, and spore development. When plants are drought-stressed, the bacteria that produce EPS make them resistant to water (Sandhya *et al*.,2009) [91]. During drought stress, compatible solutes such as glycine, proline, betain, and trehlose accumulate, assisting bacteria in maintaining membrane permeability, enzyme integrity, and protein function. When plants are drought-stressed, the bacteria that produce EPS make them resistant to water (Sandhya *et al*.,2009) [91]. During drought stress, compatible solutes such as glycine, proline, betain, and trehlose accumulate, assisting bacteria in maintaining membrane permeability, enzyme integrity, and protein function.

2.2. Brief overview of drought stress tolerance

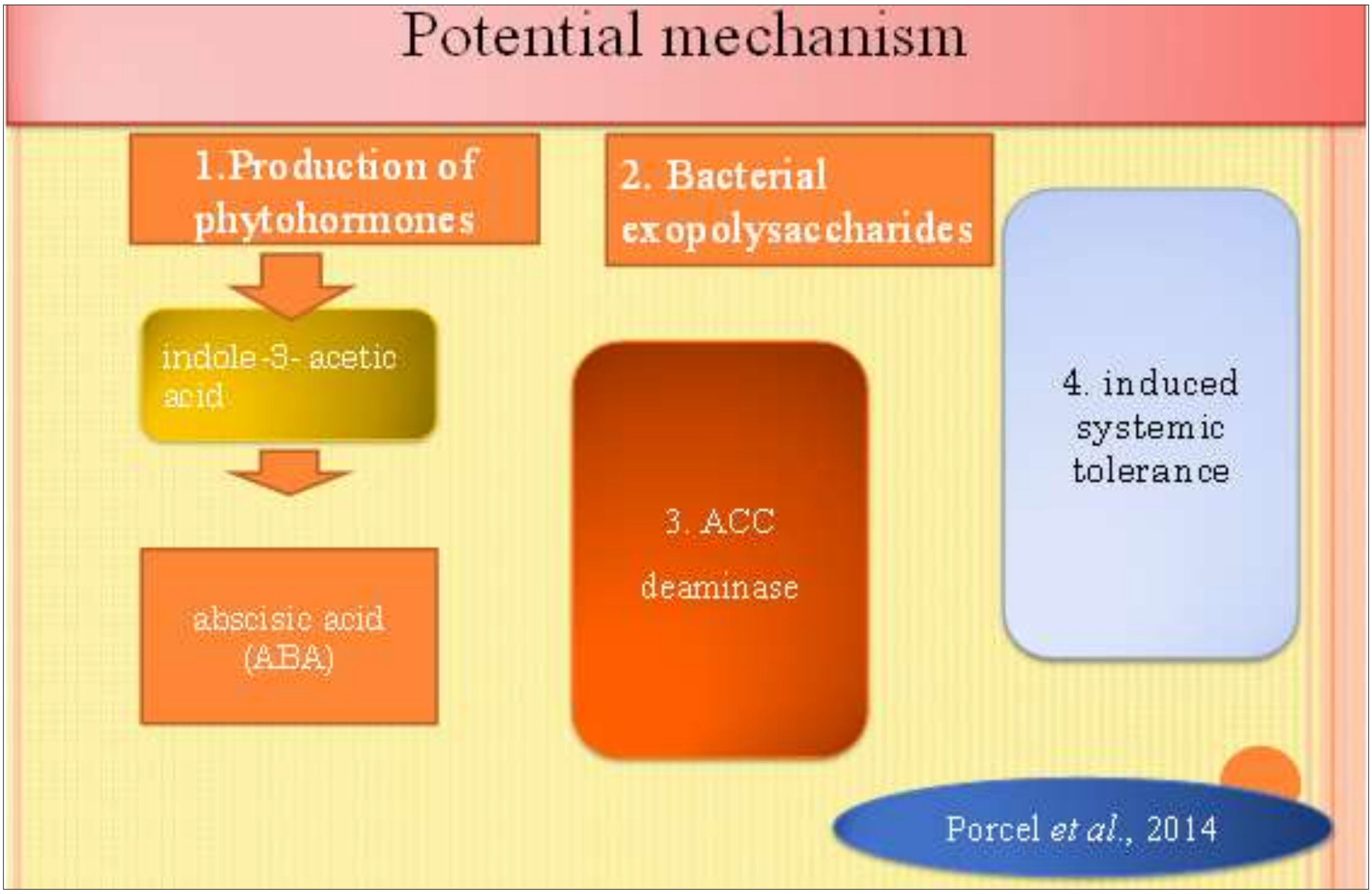


Fig 2: Potential mechanism

Table 1: Drought stress tolerance mediated by microbes

Plants	Microbes	Effect/Mechanism	References
Maize (Zea mays)	*Azospirillum lipoferum* *Bacillus* Spp.	Increase the amount of soluble sugar, free amino acids, and proline. Increase the amount of soluble sugar, free amino acids, and proline in your body. Root length, shoot fresh weight, shoot dry weight, and root fresh weight are all affected. Proline, carbohydrates, and free amino acids accumulate more, and electrolyte leakage is reduced. It also lowers antioxidant enzyme activity (Catalase, glutathione peroxidase).	Bano *et al.,* (2013) [92] Vardharajula *et al.,* (2011) [17]
Soybean	*Pseudomonas putida* H-2–3	Abscisic and salicylic acid levels should be lower, and jasmonic acid levels should be greater. Reduced superoxide dismutase, flavonoids, and radical scavenging activity, which modulated antioxidants.	Kang *et al.,* (2014) [89]
Wheat *(Triticum aestivum)*	*Azospirillum brasiliense* NO40 *Rhizobium leguminosarum* (LR-30)	Rhizobia produced catalase, exopolysaccharides, and IAA, which increased growth, biomass, and drought tolerance.	Hussain *et al.,* (2014) [93]
Lavandula dentate	*Bacillus thuringiensis*	IAA induced higher proline and K-content improved nutritional, physiological, and metabolic activities and decreased glutathione reductase (GR) and ascorbateperoxidase (APX) activity	Armada *et al.* (2014) [6]
Cicer arietinum L.	*Pseudomonas putida MTCC5279 (RA)*	Osmolyte accumulation, ROS scavenging ability and stress-responsive gene expressions	Tiwari *et al.,* (2016) [94]
Lettuce	*Azospirillum sp.*	Promote aerial biomass, chlorophyll and ascorbic acid content, better overall visual quality, hue, Chroma and antioxidant capacity, and a lower browning intensity	Fasciglione *et al.*, 2015 [24]
Arabidopsis	*Azospirillum brasilense* Sp 245 *Phyllobacterium brassicacearum strain* STM196	Improved plants seed yield, plants survival, proline levels and relative leaf water content; it also decreased stomatal conductance, malondialdehyde and relative soil water content Enhanced ABA content resulted in decreased leaf transpiration, delay in reproductive development, increased biomass and water use efficiency	Cohen *et al.,* 2015 [48] Bresson *et al.,* 2013 [95]
Brassica oxyrrhina	*Pseudomonas libanensis TR1 and Pseudomonas reactans Ph3R3*	Plant growth, leaf relative water, and pigment content increased, but proline and malondialdehyde concentrations in leaves declined.	Ma *et al.,* 2016 [54]
Rice (*Oryza sativa* L.)	*Trichoderma harzianum*	enhance root development regardless of water availability and postpone drought response	Shukla *et al.,* 2012 [96]
Medicago truncatula	*Sinorhizobium medicae*	During drought stress, root nodulation and nutrient uptake are important.	Staudinger *et al.,* 2016) [97]

2.2.1 Salinity stress

One of the most common abiotic stress factors in modern agriculture is salinity stress. Due to a variety of factors, salinity has a significant impact on the majority of the world's agricultural lands. Due to the harmful effects of ions and osmotic stress, salinity reduces microbial activity, resulting in diminished plant growth and development. Salinity reduces soil water potential, making it difficult for plants to absorb water and nutrients, resulting in osmotic stress. Cations such as Na+ (sodium), Ca2+ (calcium), K+ (potassium) and anions Cl (chloride), NO3 (nitrate) induce salinity in soil under a variety of situations. Salt is found in soil as electrically charged ions as a result of insufficient rain or soil degradation (Shrivastava and Kumar, 2015) [98]. Salinity stress affects many elements of plant life, including agricultural productivity, seed germination, water and nutrient intake, as well as physicochemical and ecological equilibrium (Shrivastava and Kumar, 2015) [98]. It also has a negative impact on the nodulation process, lowering nitrogen fixation and crop output. Among these, nitrogen fixation is one of the most critical processes that is harmed by salt stress. During salinity stress, the nitrogenase enzyme, which is responsible for nitrogen fixation, is diminished. Soil salinity reduces water intake by roots from the soil, and larger levels of salt water within cells are poisonous to plants, stifling their growth. Salinity has an osmotic and ion toxicity effect on plant development and microorganism function. Fungi, unlike bacteria, are more susceptible to high salt concentrations. Plants and microorganisms have difficulty absorbing water from soil when their osmotic potential is low or high.

2.2.2 How to deal with saline stress: Farmers and agricultural scientists face a difficult problem in determining soil salinity. The accumulation of harmful Na and Cl ions in the soil, as well as nutritional imbalances, have a significant impact on plant growth and microbial activity. Inoculation with PGP microorganisms and endophytic microbes has been shown to reduce the harmful salt effect on many plants. Plant growth under salinity stress can be aided by PGP microorganisms through a variety of direct and indirect ways. Furthermore, the biofilm generated by PGPB under salinity stress is useful in reducing the negative effects (Kasim *et al.*, 2016) [99]. In comparison to the control insaline condition, Azospirillum inoculated lettuce seed showed superior germination and vegetative growth (Barassi *et al.*, 2006) [100]. In another study, inoculating salttolerant and salt sensitive chilli pepper plants with the growth-promoting bacteria Pseudomonas stutzeri reduced the harmful effects of soil salinity (Bacilio *et al.*, 2016) [10]. In another study, inoculating salttolerant and salt sensitive chilli pepper plants with the growth-promoting bacteria Pseudomonas stutzeri reduced the harmful effects of soil salinity (Bacilio *et al.*, 2016) [10]. While certain microbial species reduce the activity of biofilm development on barely grains due to alkalinity stress, others do not (Kasim *et al.*, 2016) [99]. The co-inoculation of AM fungus with salt-tolerant bacteria improves salinity tolerance in some plants dramatically. The co-inoculation of *R. intraradices* and *Massilia* sp. RK4 renovate Arbuscular mycorrhizal fungi (AMF) root colonisation and nutrient accumulation in maize plants under salt stress, for example. These fungal and microbial interactions have a big influence on maize plant salinity tolerance (Krishnamoorthy *et al.*, 2016) [101].

Table 2: Mode of action Microbial mediated salinity stress tolerance

Plants	Microbes	Effect/Mechanism	References
Groundnut	*Brachybacterium saurashtrense* (JG-06), *Brevibacterium* casei (JG-08)	Greater Ca2+, phosphorus, and nitrogen content, as well as a higher K+/Na+ ratio. Auxin concentrations are higher in the shoot and root.	Shukla *et al.*,(2012) [96]
Mung bean	*Rhizobium and Pseudomonas*	Under natural salt-affected conditions, ACC-deaminase improved mung bean growth, nodulation, and yield.	Ahmad *et al.*,(2011) [4]
Barley and oats	*Acinetobacter* spp. and *Pseudomonas* sp.	Plant development is aided by the enzyme ACC deaminase, which reduces ethylene and promotes IAA production.	Chang *et al.*,(2014) [21]
Wheat	*Azospirillum* Sp. *Pseudomonas* Sp. *Serratia* Sp.	Increased grain yield and dry weight of the shoots. To maintain osmotic balance, plants acquire some organic solutes (e.g. proline and soluble carbohydrates) as well as inorganic ions.Reduce ethylene levels, increase plant height, root length, and yield by having ACC deaminase activity.	Zahir *et al.*, (2009) [102]
Maize (*Zeya mays*)	*Pseudomonas* and Enterobacter	Reduces the triple response	Nadeem *et al.* (2009) [39]
Rice GJ-17	*Pseudomonas pseudoalcaligenes*	Reactive oxygen species toxicity has been reduced (ROS)	Nadeem *et al.*, (2009) [39]
Rice	*Bacillus amyloliquefaciens* NBRISN13(SN13)	Differential transcription modulation	Nautiyal *et al.*, (2013) [29]
Barley	*Hartmannibacter diazotrophicus* E19	Root and shoot dry weights have increased.	Suarez *et al.*, (2015) [26]
lettuce seeds	*Azospirillum*	Higher biomass, ascorbic acid, and Promoted	Fasciglione *et al.*, (2015) [24]
Maize	*Pseudomonas putida* UW4	As a result, the length of the shoot grows.	Cheng *et al.*, (2011) [103]

2.3 Mode of action of salinity stress tolerance

The stimulation of growth under stress conditions is aided by the diversity of salinity stress resistant microorganisms (Table 2). Phytohormone production (e.g. auxin, cytokinin, ethylene, and gibberellins), nitrogen fixation, nutrient mobilisation, and siderophores production are examples of direct methods (Hayat *et al*., 2010) [15]. They each have a unique mechanism and mode of operation. These mechanisms cause root length, surface area, and root number to increase, resulting in increased nutrient uptake (Egamberdieva and Kucharova, 2007) [104]. Reduced frequency of disease-causing plant pathogens is a primary indirect factor. Rhizobacteria that colonise the roots create ACC deaminase, which converts ACC to ammonia and alpha ketobutyrate, lowering ethylene. Under stress, the enzyme Rhizobitoxine inhibits ethylene synthesis and promotes nodulation, according to Vijavan *et al.* PGPB reduce salt stress by collecting osmolytes in their cytoplasm, which counteract osmotic stress and keep cell turgor and plant development under check. Microbial EPS confers resistance to salinity by binding to cations, rendering it unavailable to plants during times of stress (Vardharajula *et al*., 2011) [17]. Co-inoculation with PGPR strains like Rhizobium and Pseudomonas can help plants flourish in saline soil by overcoming these negative effects (Bano and Fatima, 2009) [13, 19]. PGPR features were found in two rhizospheric bacteria isolated from saline soil, *Bacillus pumilus* and *Bacillus* subtilis, including IAA synthesis, ammonia and hydrogen cyanide (HCN) generation, phosphate solubilization, and salt stress resistance (Damodaran *et al*., 2013) [18]. PGPR, Rhizobium, and Pseudomonas ameliorate salt stress in NaCl-affected maize plants, according to Bano and Fatima (2009) [13, 19]. Reduced electrolyte leakage, osmotic potential, increased proline synthesis, and selective uptake of K ions all contribute to maize plant stress resistance. Rice plants treated with *P. pseudo* alcaligenes and *Bacillus pumilus* had improved salinity tolerance and have greater glycine beta line concentrations (Jha *et al*., 2011) [20]. Induced systemic tolerance (IST), or increased tolerance to salinity stress, is the outcome of PGPR-induced physical and chemical alterations. They enhance root and shoot growth in cotton plants and lower disease susceptibility to fungus like Fusarium solani. It also made cotton resistant to the red rot disease (Egamberdieva *et al*., 2015) [104]. In wheat crops under water salt stress, salinitytolerant Azospirillum strains stimulate plant growth and increase total plant dry weight, grain weight, and other metrics (Nia *et al*., 2012) [23]. In maize plants, the plant hormone ABA plays a crucial role in salinity stress by acidifying the apoplast. Under stressful conditions, Azospirillum-inoculated lettuce seed promotes growth, product quality, and storage life (Fasciglione*et al*., 2015) [24]. Under saline conditions, *Hartmannibacter diazotrophicus* E19, a PGPR isolated from Plantagowinteri, promotes barley (*Hordeum vulgare* L.) plant development (Suarez *et al*., 2015) [26]. Pseudomonas alcaligenes PsA15, *Bacillus* polymyxa BcP26, and Mycobacterium phlei MbP18 are three PGPR isolates that have been shown to thrive insaline soils such as calcisol soil by Egamberdiyeva (2007) [16, 25]. Increased proline content, decreased electrolyte leakage, maintenance of relative water content of leaves, and selective uptake of K ions improved salt tolerance in Zea mays after co-inoculation with PGPB, Rhizobium, and Pseudomonas (Bano and Fatima, 2009) [13, 19]. Three PGPR strains were identified from the tomato rhizosphere with higher sodium chloride concentrations: *P. fluorescens*, *P. aeruginosa*, and *P. stutzeri*. These bacteria have the ability to increase salinity tolerance in tomato plants by inducing the synthesis of phytohormones and the ACC deaminase enzyme (Bal *et al*., 2013; Tank and Saraf, 2010) [11, 27, 28]. The salttolerant *Bacillus* amyloliquefaciens NBRISN13 (SN13) inoculated with rice plant increases growth and salt tolerance by up-regulating and repressing 14 genes in rice plants, according to Nautiyal *et al*., (2013) [29]. Salinity stress tolerance is also induced in plants by phytohormone-producing endophytic bacteria. Salinity stress tolerance in Oryzasativa has been found to be induced by ABA and auxin generated by *Bacillus* amyloliquefaciens RWL-1 (Shahzad *et al*., 2017) [30]. In Solanum pimpeli folium, plant growth enhancing endophytic bacteria combined with exogenous jasmonic acid offset the unfavourable influence of salt (Khan *et al*., 2017) [31]. (Table 2). The role of the tricarboxylic acid (TCA) cycle in tomato plant salt tolerance is another factor to consider when developing resistance to salinity tolerance (Torre-González *et al*., 2017).

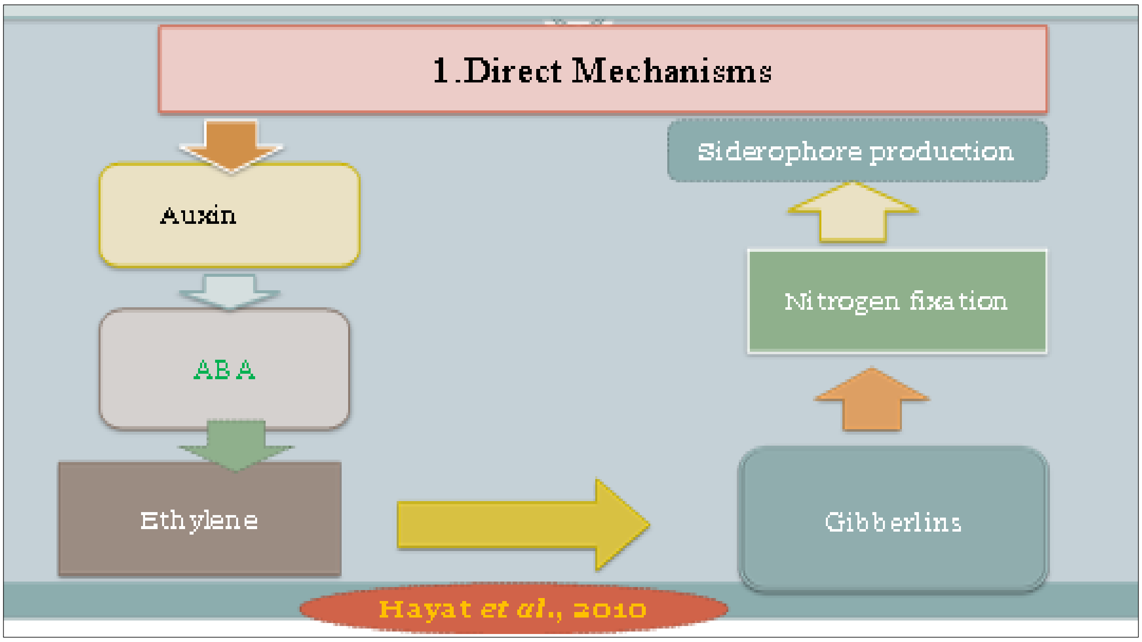


Fig 3: Mechanis7m of salinity stress tolerance

2.3.1Salinity and drought stress Interaction

Secondary stress, such as oxidative and osmotic stress, results. PGPB induces systemic resistance to salinity and drought stress by modulating physiological and biochemical processes. Phytohormone levels, antioxidant generation, and osmotic adjustment are all important steps in the defence process. Compatible osmolytes are created by microbial strains and plants in response to salinity and drought stress to stimulate plant growth. During salinity and drought stress, plants stimulated by microorganisms increase proline synthesis.

2.4 Salinity and drought stress tolerance are mediated by mycorrhizal fungi

Drought and salinity stress tolerance are aided by plant-associated fungus. Drought stress is alleviated by AM symbiosis, which changes hormone physiology and plant physiology. It also boosts photosystem II efficiency and photosynthetic product when there is a lack of water (Ruiz-Lozano *et al*., 2016) [49]. In rice plants, Trichoderma harzianumencourages root development despite low water content and prevents drought response (Shukla *et al*., 2012a, 2012b) [50, 51]. Strigolactone levels rise in lettuce and tomatoes to alleviate drought stress by developing symbiosis and improving drought tolerance (Ruiz-Lozano *et al*., 2016) [49]. AM fungus have also been identified as a key component in reducing soil salinity. Inoculation with AM has been shown to improve plant development in salt stress conditions. In a saline environment, they impede the uptake of Na or Cl by citrus plants (Navarro *et al*., 2014) [52]. As a result, inoculation with PGPR and other microorganisms could be used to alleviate salinity stress in salt-sensitive crops. Co-inoculation of PGM bacteria and plantassociated fungus may improve the effectiveness of drought and salinity stress tolerance.

2.4.1 Heavy metals stress

Heavy metal pollution in soil is caused by continued industrialization, intensive agricultural methods, and anthropogenic activities. Heavy metals have a negative impact on plants as well as human health. Heavy metals are non-degradable metals with a density more than 4 g/cm3 that are also toxic at low concentrations (Duruibe *et al*., 2007; Ma *et al*.,2016a) [53, 54]. It is critical to eliminate these heavy metals in a sustainable and effective manner in order to protect and save the ecosystem from their hazardous effects. Because the majority of remediation approaches are both expensive and harmful to soil structure (Glick, 2010) [58, 66]. Plants and their associated bacteria are used in phytoremediation, an emerging technology for removing heavy metals from soil. Furthermore, it is a cost-effective and long-term solution for heavy metal removal (Ma *et al*., 2016) [54].Microbes, on the other hand, improved the efficacy of phytoremediation. Microbes are more sensitive to heavy metal stress than other living organisms, and they may be an excellent indicator of it (Broos*et al*., 2004; Chen *et al*., 2014) [56, 57]. Because of its cheap cost, environmentally safe, and attractive approach, as well as its application in a variety of situations, the use of microbial diversity for assisting heavy metals remediation has gained popularity in recent years.

2.4.2 Microbial mediated heavy metals stress tolerance

Rhizobacteria, mycorrhiza, and firmicutes are only a few of the heavy metal resistant microorganisms and plant-associated microbes that can help plants grow and thrive amid metal stress (Table 3). Efflux, metal impermeability, volatilization, EPS sequestration, metal complexation, and enzymatic detoxification are all methods involving these bacteria. Furthermore, these plant-associated bacteria help plants grow and develop by reducing ethylene levels, producing plant growth regulators like IAA and ACC deaminase, and suppressing disease (Glick, 2010) [58, 66]. Nitrogen fixation, nutrient mobilization, siderophores, and phosphate solubilization, among other things, help plants grow and remove heavy metals. Heavy metals have been removed using both live and non-living microbial biomass. The characteristics of bacterial, fungal, and fungal cell walls, as well as their functional groups, are of great significance. Microorganism bioaccumulation is a powerful way for removing heavy metals from contaminated soil. Proteobacteria, Firmicutes, and Actinobacteria have been observed to remove larger concentrations of Mn, Pb, and As from metal-polluted soil (Zhang *et al*., 2015) [59]. Fatnassi*et al*. (2015) [60] reportedthat copper (Cu) concentrations more than 1 mM harmed Viciafaba plant growth, but that inoculating with rhizobia and PGPR decreased the impacts. AM fungi reduce malonaldehyde and hydrogen peroxide, minimising the negative effects of cadmium stress. Jing *et al*. (2014) [105]shown that Enterobacter sp. and Klebsiella sp. are efficient metal tolerant by creating plant growth chemicals when removing Cd, Pb, and Zn metal from polluted soil (Table 3).

Another study found that cadmium resistant PGPB, Micrococcus sp. MU1, and Klebsiella sp. BAM1 improve cadmium mobilisation and promote root elongation and plant growth in contaminated soil by Prapagdee*et al*., 2013 [61]. Phosphate solubilization increases plant development and nutrient absorption by Arsenic resistant bacteria (ARB) from Pterisvittata, which is an excellent siderophore generator. Two bacterial species, *Bradyrhizobium japonicum* E109 and *Azospirillum brasilense* Az39, colonised in arsenic (As) contaminated soil, accumulated As in cell biomass, and promoted plant growth, according to Armendariz *et al*., (2015) [7]. As a result, PGPR either aids plant development under heavy metal stress or prevents heavy metal assimilation in plant tissue brought into the cytosol Siderophores iron complexes enter the cytosol at a higher rate than other heavy metals. Other microbes found inside plant tissues, like rhizobacteria, may help with phytoremediation. Endophytic bacteria, for example, exhibit metal resistance qualities and stimulate plant development under metal stress by supplying mineral nutrients, plant growth regulators, and enzymes directly to the plant. Endophytic bacteria are less effective than rhizosphere bacteria at producing siderophore. Endophytic microorganisms can produce Nitrogenase enzyme in the presence of metals and low nitrogen levels by giving nitrogen to related plants. Dory *et al*.2001 identified stem endophytic taxa Burkholderia, Rahnella, Sphingomonas, and Acinetobacter from Populustrichocarpa and Salixsitchensis, which produce Nitrogenase enzyme and can fix atmospheric nitrogen. Endophyticbacteria improve the rate of nitrogen fixing under long-term nitrogen shortage. Endophytic bacteria produce phytohormones (mostly auxin), which promote root development and nutrient uptake. Other low molecular weight organic acids generated by PGPM also play an important role in phytoremediation. Gluconic, oxalic, and citric acids are the most effective at mobilising heavy metals and making them available to plants. Furthermore, oxidation or reduction reactions have a significant impact on the mobility of heavy metals such as As, Cr, Hg, and Se. When compared to low oxidation states, several metals are less soluble in higher oxidation states. Metalloid solubilization is regulated by both oxidation state and ionic form. Bio-methylation is another approach for heavy metal mobilisation that involves the transfer of a methyl group via bacterial action. Many bacteria are involved in the methylation of Pb, Hg, Se, As, Tn, and Sn. Phytochelatins (PCs) are metal-binding cysteine-rich peptides produced by glutathionein in response to heavy metal stress in various fungi and plants.

Table 3: Mode of action ofMicrobial mediated heavy metals stress tolerance

Heavy Metals	Plants	Microbes	Effect/Mechanism	References
Cd, Ni, As, Cu, Pband Zn	*Alnus firma*	*Bacillus thuringiensis GDB-1*	Production of phytohormones, siderophore, (ACC) deaminase, and Phosphorus solubilization	Babu *et al*. 2013 [9]
Cd and Pb	*Gladiolus grandiflorus* L.	*ThioBacillus thiooxidans* and *Pseudomonas putida*	Increase root length, plant height, plant dry biomass, and Cd and Pb accumulation.	Mani *et al*. 2016 [63]
Cd, Zn and Cu	*Solanum nigrum* L.	*Pseudomonas* spp. Lk9	Improved soil availability of iron, phosphorus, and heavy metals, as well as shoot dry biomass and biosurfactant uptake of Cd, Zn, and Cu.	Chen *et al*. 2014 [57]
Cd, Zn and Cu	Sedum	*Bacillus pumilus* E2S2,	Phosphorus solubilization, IAA production, siderophores, and ACC deaminase	Ma *et al*. 2015 [64]
Cd and Pb	Lettuce	*Bradyrhizobium japonicum*	IAA synthesis boosts growth and increases shoot root lengths as well as dry biomass.	Seneviratne *et al*. 2016 [65]

2.4.3 IPGPM aids in the elimination of heavy metals

Phytoremediation is more advanced than older approaches, and using PGPM to remove heavy metals from polluted soil can improve their efficiency (Glick, 2010) [58, 66]. For heavy metal removal, this procedure is the most successful, innovative, and healthy. PGPB accessible metals for buildup and removal through chemical and physical processes (Ullah *et al*., 2015) [67, 73]. Extracellular, intracellular accumulation, sequestration, and biotransformation of high hazardous to less harmful bacteria are the main mechanisms used by germs to cope (Babu *et al.*, 2013; Qian *et al.*, 2012) [9, 62, 68, 69]. Heavy metals can be entirely degraded by some bacteria. Pseudomonas sp. MBR, for example, shows the biotransformation and elimination of single Fe (III)–, Zn–, and Cd–citrate complexes (Qian *et al.*, 2012) [69]. PGP bacteria can help with phytoremediation in a variety of ways, both directly and indirectly.

2.4.4 Direct mode of mechanism of phytoremediation:

Solubilization, bioavailability, and accumulation of heavy metals are the primary mechanisms involved in direct aid to phytoremediation by PGPM (Vymazal and Bezinová, 2016) [70]. Plant-associated microorganisms employed various ways to remove heavy metals from metal-contaminated soil. Siderophore is a low-molecular-weight organic molecule produced by microorganisms associated with plants that chelates heavy metals and increases their availability in the rhizosphere. Its major function is in ferric iron chelation, but it also has a high affinity for metals and forms complexes that are carried into the cytosol (Saha *et al.*, 2016; Zoch *et al.*, 2016) [71, 106]. Siderophoreiron complexes are more commonly transferred into the cytosol than other heavy metals (Zoch *et al.*, 2016) [106]. Other microbes found inside plant tissues, like rhizobacteria, may help with phytoremediation. Endophytic bacteria, for example, exhibit metal resistance qualities and stimulate plant development under metal stress by supplying mineral nutrients, plant growth regulators, and enzymes directly to the plant. Endophytic bacteria are less effective than rhizosphere bacteria at producing siderophore. Endophytic microorganisms can produce Nitrogenase enzyme in the presence of metals and low nitrogen levels by giving nitrogen to related plants. Dory *et al.*,2002 found that the endophytic genera Burkholderia, Rahnella, Sphingomonas, and Acinetobacter from the Populustrichocarpa and Salixsitchensis produce Nitrogenase enzyme and can fix atmospheric nitrogen.

During long-term nitrogen deprivation, endophyticbacteria improve the rate of nitrogen fixation. Endophytic bacteria produce phytohormones (Mostly auxin), which promote root development and nutrient uptake. Other low molecular weight organic acids generated by PGPM also play an important role in phytoremediation. Gluconic, oxalic, and citric acids are the most effective at mobilising heavy metals and making them available to plants. Furthermore, oxidation or reduction reactions have a significant impact on the mobility of heavy metals such as As, Cr, Hg, and Se. When compared to low oxidation states, several metals are less soluble in higher oxidation states. Metalloid solubilization is regulated by both oxidation state and ionic form. Bio-methylation is another approach for heavy metal mobilisation that involves the transfer of a methyl group via bacterial action. Many bacteria are involved in the methylation of Pb, Hg, Se, As, Tn, and Sn. PCs are metal-binding cysteine-rich peptides produced by glutathionein in response to heavy metal stress in various fungi and plants.

2.4.5 Indirect mode of mechanism of phytoremediation

Plant growth is improved, pathogen infection is inhibited, and heavy metal accumulation is increased as a result of the indirect support. Heavy metal concentrations in the rhizosphere disrupt nutrient uptake and limit plant growth. Plant growth-promoting microorganisms may be able to offer nutrients in such a restricted environment. Through a symbiotic relationship, PGPB fixes atmospheric nitrogen and provides for plant under metals stress conditions (Nonnoi *et al.,* 2012). Another key element present in abundance in the soil in a complex form that is unavailable to plants is phosphorus. Phosphorus is typically found in insoluble form in the soil. Microbes create organic acids, which are soluble in acid and supplied to plants. Endophytic bacteria help plants grow in metal-stressed environments by suppressing diseases or inducing systemic resistance. Overall, microbial diversity aids in the elimination of heavy metals from polluted environments, as well as the growth and development of plants. Microbes with significant phytoremediation abilities help the plant live in a heavy metal environment more easily and play a key role in growth promotion.

2.5 Phytoremediation with the help of PGPB and AM fungi

PGPM has been shown to help in phytoremediation in a vast number of cases. The utilisation of bacteria that convert heavy metals into bio available and soluble forms through the action of siderophores, organic acids, bio surfactants, bio methylation, and redox reactions aids phytoremediation of heavy metals by diverse plants (Ullah *et al.*, 2015) [67, 73]. Heavy metals can cause a 30–35 percent reduction in plant length, bulk, and shoot-to-root ratio. The PGPR vaccine restores and improves growth and output (Pishchik *et al.*, 2009) [74]. The inclusion of PGPB improves phytoremediation efficiency. Most plants have a symbiotic relationship with AM fungi, which improves their ability to absorb water and nutrients from the soil (Miransari, 2011) [75]. In addition, using *Bacillus*, *Lysinibacillus*, and Pseudomonas chelates in combination with heavy metals resistance bacteria, *Bacillus*, *Lysinibacillus*, and Pseudomonas chelates, phytoremediation of heavy metals might be improved. Microbe-produced phytochelatins have the ability to bind to heavy metals, allowing them to be removed from the environment. Schizosaccharomyces pombe and *Pseudomonas putida* KT2440 clones increase heavy metal accumulation in a polluted heavy metal environment (Yong *et al.*, 2014) [76].

2.5.1 Stress caused by high temperatures

Temperature stress has become more common and intense as a result of climate change. Heat stress (HS) and cold stress (CS) are becoming major abiotic stress conditions for crop productivity and food security around the world. Changes in the plasma membrane, water content (Transpiration), reduced photosynthesis activity, enzyme functioning, cell division, and plant development are all key effects of temperature stress. Climate change has the biggest influence in tropical and subtropical regions, including India (Rodell *et al.,* 2009; Alam *et al.,* 2017) [77, 5]. Different components of the cell and the cell membrane may be affected by temperature. Heat, for example, can make them more fluid, but cold can make them more rigid. If not appropriately handled, heat stress is a result of a variety of physiological and biochemical factors. One of the most acute abiotic stresses, heat stress produces significant changes in plant hormone concentrations and responses. "During times of stress, the concentration of jasmonic acid (JA) increases dramatically. Crop tolerance is controlled by numerous regulatory mechanisms in plants. Countless plant species have adapted to both low and high temperatures. Plant species undergo a variety of physiological changes as a result of the changing environment, allowing them to acclimate and thrive in a variety of temperature conditions. To combat heat stress, plants use a variety of processes, including the creation and storage of enzymes and osmolytes." Heat shock proteins (HSP20, HSP60, HSP70, HSP90, and HSP100) and ROS-scavenging enzymes (Ascorbateperoxidase and catalase) are important functional proteins. However, the majority of crops were unable to withstand high temperatures, including heat stress and cold shock. As a result, there is a pressing demand for such a severe temperature tolerance mechanism.

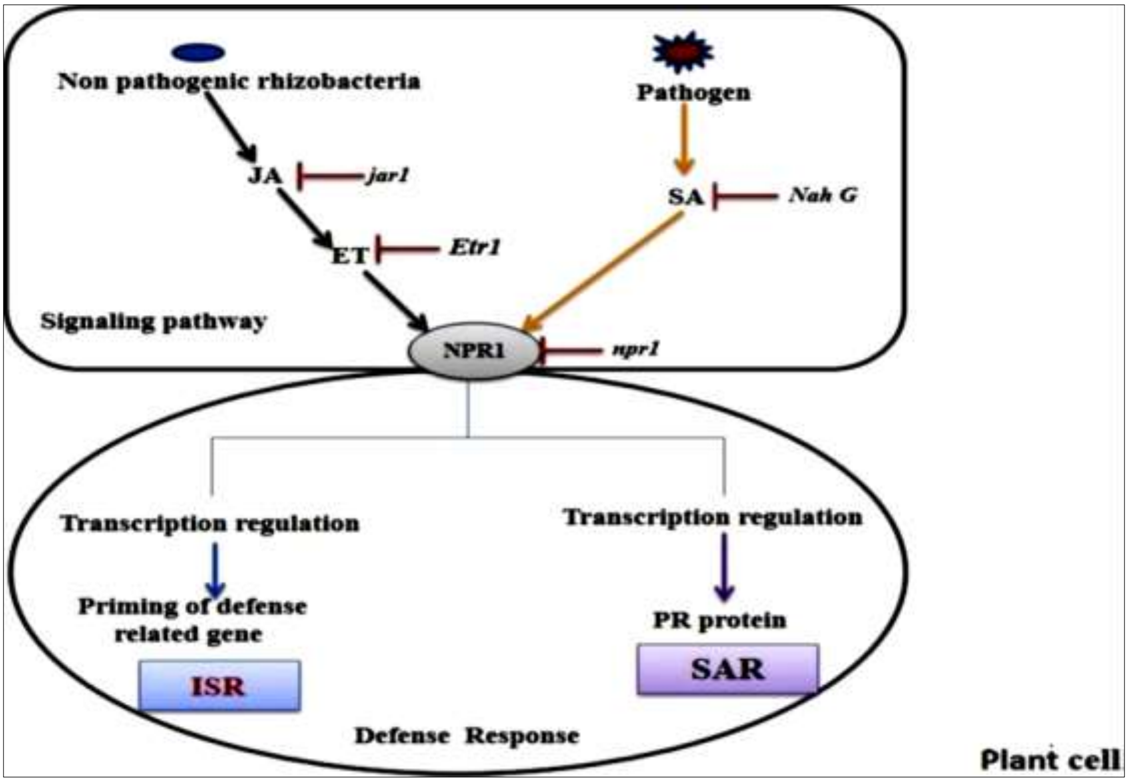
2.5.2 Microbes under stress due to temperature

There is a pressing need to find a solution for crop production in the face of climate change. Microbes to is one method for reducing the negative effects of heat and cold stress. In extreme temperatures, temperature has a vital role in regulating the physiology and metabolism of microorganisms. The ability of microorganisms to adapt to low and high temperatures is aided by their enzymatic properties. These microorganisms have developed excellent mechanisms to protect their protein, membrane, and nucleic acid in order to survive in such environments. Under these conditions, gene expression of heat and cold resistant proteins and enzymes is increased. Molecular chaperons are one of the most effective heat-resistance mechanisms. Microbes are split into two groups based on their growth: psychrophilic and psychotrophic bacteria. Psychrophilic microorganisms grow best at or below 15 °C, whereas psychotrophic microbes grow best at or above 15 °C. Heat stress enhanced the expression of a gene involved in microbial survival. "Heat stress increases the expression of the DnaK gene in *Alicyclobacillus* acidoterrestris, which codes for HSP, which protects microorganisms against heat. It grows from 23 to 70 years old, with a peak at 45–50 years old. HSP expression is a technique for coping with extreme temperatures. Heat shock protein induction is a crucial strategy for surviving under extreme heat stress. They survive heat stress by obtaining effective nutrition and water intake, as well as increasing photosynthesis. Trehalose production is activated under heat stress and protects microorganisms against heat, cold, and oxidative damage. During heat stress, the accumulation of trehalose in bacteria and fungi increases by a factor of ten". Trehalose accumulated in microbial cells protects them from thermal harm during heat stress and cold shock (Li *et al.*,2009) [78]. It is important for protein stability in cells. Trehalose decreases heat stress-induced protein denaturation and aggregation in fungus, allowing the protein to keep its original shape. Trehalose can also help preserve proteins from heat-induced denaturation. Trehalose has been shown to be particularly effective against freezing and desiccation. During drought stress, the amount of metabolites produced by microorganisms changes depending on the plant and microbe.

3. Heat stress tolerance is mediated by a number of different mechanisms

High and low temperature tolerance bacteria have effectively colonised the majority of the earth's biosphere. Microbes that have evolved to low temperatures have plant growth capabilities. *Pseudomonas cedrina*, *Brevundimonas terrae*, and Arthrobacternicotianae adapted for low temperature demonstrate multifunctional plant growth stimulating potential, according to Yadav *et al.*, (2014) [79]. In low temperature, the PGPR isolated from the root nodule of a low temperature growing pea plant has good bio fertilizer ability (Meena *et al.*, 2015) [80]. Psychrophilic bacteria isolated from Antarctica also have antibacterial action, according to Javani *et al.*, (2015) [81]. Inoculation of temperature tolerant phosphate solubilizing microorganisms into agricultural fields, on the other hand, works as a multifunctional bio fertiliser. In the agricultural field, it serves as a biogeochemical phosphorus cycle system. Phosphate-solubilizing microorganisms' primary purpose is to convert insoluble phosphorus to soluble forms via acidification. JA: Jasmonic Acid; ET: Ethylene; SA: Salicylic Acid; NRP: Nonexpresser of PR genes; ISR: Induced Systemic Resistance; SAR: Systemic Acquired Resistance: JA: Jasmonic Acid; ET: Ethylene; SA: Salicylic Acid; NRP: Nonexpresser of PR genes A key mechanism for biotic stress tolerance is the production of reactive oxygen species (ROS) and oxidative burst (Miller *et al*., 2010) [82]. Induce systematic resistance (ISR) and systemic acquired resistance are the two types of defensive reaction mechanisms engaged by microorganisms (SAR).

Non-pathogenic root associated plant growth boosting bacteria may increase the ISR, whereas SAR involves changes in molecular gene expression and is linked to pathogenesis related (PR) proteins. ISR and SAR gene induction and expression differ depending on the eliciting and regulatory pathways (Nawrocka and Maolepsza, 2013) [83]. Under biotic stress, PGPM triggers SAR, which involves the accumulation of PR proteins and SA, whereas ISR relies on pathways regulated by jasmonate and ethylene (Salas-Marina *et al.*, 2011; Bari and Jones, 2009) [84, 107]. SA, JA, and ET production are heavily influenced by reactive oxygen species (ROS) and create a complex network to modulate pathogens (. Ethylene and a regulatory factor play a key role in PR gene expression. The induction of resistance in plants is determined by the elicitor generated by non-pathogenic microorganisms and the interplay of these molecules.



3.1 Induced systemic resistance

Infection with microbes such as bacteria, fungus, or viruses can cause the plant to develop resistance to future attacks, which is known as induced systemic resistance (Heil, 2001) [85]. Phytopathogen-induced systemic resistance immunises plants against a wide range of diseases. Through the formation of the allopathic substance, competition for ecotype and nutrition, systemic resistance was induced, which was accompanied by PGPM. Antibiotics and allelochemicals, such as siderophores, are effective against pathogens and restrict their growth (Jain *et al.,* 2013) [86].

In response to pathogen Fusarium sp. causing wilt disease in carnations (*Dianthus caryophillus*) and cucumber (*Cucumis sativus*) in response to pathogen *Colletotrichum orbiculare* causing foliar disease, PGPM induced defence mechanisms were first reported in response to pathogen Fusarium sp. causing wilt disease in carnations (*Dianthus caryophillus*) and cucumber (Cucu (Compant *et al*.,2005) [87]. Lee observed that root associated *amyloliquefaciens* strain HK34 effectively generated resistance against *P. cactorum* in his investigation on the production of systemic resistance in Panax ginseng against Phytophthora. Induced systemic resistance is also used by Pseudomonas and *Bacillus* strains to manage plant disease in various crops.

3.2 The use of stress-tolerant microorganisms in agriculture and industry

3.2.1 Bio-fertilizers

Bio fertilizers are a mixture of living microorganisms with the potential to convert inedible nutrients into useable nutrients through a biological process. They could be employed as a bio fertiliser because of their capacity to boost plant development in both abiotic and biotic conditions. Biofertilizer microorganisms have the ability to convert atmospheric nitrogen to ammonia and phosphate solubilization in the rhizosphere of plants. Biofertilizers are living organism-containing compounds that, when inoculated with seed or plant, aid in the growth and development of the plant. Stress-tolerant PGPM play an important role in nutrient mobilisation and nitrogen fixation in the atmosphere (Kantachote *et al.,* 2016) [108]. It could be used to replace inorganic fertilisers and insecticides. Azospirillum, Acetobacter, *Azotobacter*, and Pseudomonas are only a few of the active bacteria. Furthermore, under stress conditions, Pseudomonas and *Bacillus* spp. are effective biocontrol and plant growth promoters (Kumar *et al.*, 2014) [43]. They protect plants from infections and help them withstand disease. These microorganisms enhance nutrition availability, nutrient competition, and systemic resistance. Biofertilizers are utilised commercially all over the world. As a result, inoculating stress-tolerant microorganisms as a multifunctional biofertilizer in agricultural fields could be a viable alternative to inorganic fertilisers and pesticides. Finally, biofertilizers have a positive impact on plant growth, yield quality, nutrient mobilisation, soil health, and disease susceptibility due to environmental change. As a result, in the next years, selecting effective microorganisms and formulating biofertilizers for a changing environment could be advantageous. a viable solution to the depletion of non-renewable energy sources Microbes that are thermo tolerant or themo philic are employed in the fermentation process to produce bio ethanol. *Clostridium thermowell*, *Clostridium thermohydrosulfuricum, Clostridium thermosaccharolyticum, Caldicellulosiruptor* sp., *Thermotoga* sp., *Thermoanaerobacter brockii*, *Thermoanaerobacter ethanolicus, T. thermal hydrosulfuricus, T. mathranii* are examples of thermotolerant bacteria (Arora *et al.*, 2015; Salim*et al.*, 2015) [8, 109]. *Cocus nucifera* milk, *Ananas comosus* juice, and tuna juice are used to help yeast *Saccharomyces cerevisiae* CDBB 790 produce bioethanol. Furthermore, phytoremediation of heavy metals from soil aids in long-term crop production and has a good impact on the soil. Many skin and blood illnesses in humans are caused by metal deposition in agricultural food products. Microbes aid in the removal of hazardous heavy metals from soil and limit plant absorption.

4. Conclusion and prospects for the future

Plant growth characteristics, productivity, and survivability are all affected by many types of biotic and abiotic stressors. Those crops and plants that can change their physiological and biological properties due to the expression of cold, heat, drought, salinity, and alkalinity tolerant proteins can withstand stress conditions. Crop output, food quality, and global food security are all hampered by these pressures. Hormonal imbalances, nutrient mobilisation, ion toxicity, and disease susceptibility continue to wreak havoc on plant growth and development in the current climate. The only other option for dealing with plant stressors is to develop microbiological tools and procedures for plant-microbe-soil interaction. Under abiotic and biotic stress conditions, a stress-tolerant microbial consortium of PGPM strains and mycorrhizal fungi could be employed to boost plant growth. These bacteria may help plants grow by regulating plant hormones, improving nutrition, producing siderophores, and boosting the antioxidant system. Induced ASR and ISR during numerous stressors are the other mechanisms. AM increased stress tolerance by increasing food and water supplies during stressful situations? Microbes have the ability to alleviate future food security issues while also preserving soil health. As a result, bacteria may play a vital role as an ecological engineer in resolving environmental stress problems, according to the current review.

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