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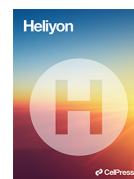
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Review article

Bioinoculants as mitigators of multiple stresses: A ray of hope for agriculture in the darkness of climate change

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ABSTRACT

Plant encounters various biotic and abiotic stresses, that affect agricultural productivity and reduce farmer's income especially under changing global climate. These environmental stresses can advance plant senescence by inducing osmotic stress, nutrient stress, hormonal imbalance, production of oxygen radicals, and ion toxicity, etc. Additionally, these stresses are not limited to plant health but also deteriorate soil health by affecting the microbial diversity of soil. To tackle this global delinquent of agriculture, several methods are suggested to ameliorate the negative effect of different types of stresses, the application of beneficial microorganisms or bioinoculants is one of them. Beneficial microorganisms that are used as bioinoculants not only facilitate plant growth by fulfilling the nutrient requirements but also assist the plant to withstand these stresses. These microorganisms produce certain chemicals such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, phytohormones, antioxidants, extracellular polysaccharide (EPS), siderophores, antibiotics, and volatile organic compounds (VOCs), etc. which help the plants to mitigate various stresses. Besides, these microbes also activate plant defence responses. Thus, these bioinoculants can effectively replace chemical inputs to supplement nutrient requirements and mitigation of multiple stresses in plants.

1. Introduction

Continuous change in climate is the most pressing issue confronting humanity today, affecting not just human health but also plant health, and has become a limiting factor for agricultural productivity. Contribution of anthropogenic activities is much higher than that of natural global climate change factors. The majority of plants are unable to adapt quickly enough with the rapid changes in ecosystems induced by global warming. The rising temperature (about 4 °C) in the late twentieth century led to a worldwide decline in staple cereals viz. wheat, rice, and maize output, as well as increased food consumption, posing a severe challenge to food security (Fiodor et al., 2021; Shew et al., 2020; Zhao et al., 2017). The effects of global warming on agricultural productivity have become a prominent focus of studies for researchers in recent decades. Nevertheless, plants will be subjected to many abiotic and biotic stresses at the same time, making their responses more complicated due to the overlapping of distinct stress response pathways (Fiodor et al., 2021).

In developing countries with growing population, crop production must be enhanced to feed the growing population. However, crops encounter many biotic and abiotic stresses, that includes high salinity, extreme temperatures, flooding, heavy metals, radiation, drought, and a variety of pests such as viruses, bacteria, fungus, insect predation, etc., that significantly reduce the development of plants by affecting their metabolic processes. Some of the key cellular alterations that occur in response to abiotic stress include impaired organization and dynamics of cytoskeleton, varying cell wall and apoplastic gap thickness, shrinking protoplasm, disturbed or swollen thylakoid membrane, and dispersed mitochondrial membrane potential along the stretched cristae (Wang et al., 2011). The cytoskeleton's organisation and dynamics are crucial in plants' reaction to a variety of abiotic stresses. Although, under adversities the functions of cytoskeleton get impaired. For instance, environmental and cellular imbalance of Na⁺ ion is a crucial factor for cortical microtubule restructuring by depolymerization first and subsequently repolymerization. However, the number of cells with repolymerized microtubules are few under higher salinity (Wang et al., 2011).

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According to Lin et al. (2014), NaCl concentrations as high as 250 mM are deadly and stimulate microfilament disintegration. According to Soda et al. (2016), heavy metals like lead (Pb) and copper (Cu) interrupt cell division during interphase by distorting mitotic spindles and causing chromosomes to migrate erroneously. Pb/Cu trigger depolymerization of microtubules and the formation of aberrant microtubule arrays with skewed, wavy microtubule bundles, and ring-like aggregates of tubulin. Similarly, plant cell cytoskeletal microfilament depolymerizes in response to heat shock, with the actin cytoskeleton actively involved. Several cytoskeletal components, including actin filaments and microtubules, are altered in terms of isoform accumulation, which impacts pollen tube germination, growth and protein localization, dependent on cytoskeleton integrity and dynamics (Çetinbaş-Genç, 2020). Unlike heat stress, cortical microtubules and polymerized microfilaments depolymerize in response to cold stress. In addition, cell wall enzyme activity and plasma membrane fluidity of the plant cell is reduced. However, tubulin expression patterns shift and more resistant cold-stable microtubules are formed (Ma and Liu, 2019; Soda et al., 2016). Most of the stresses induce the formation of reactive oxygen species (ROS) exponentially, causing cellular damage by degrading lipids, proteins, nucleic acids, inactivating enzymes, and may also induce programmed cell death (Sachdev et al., 2021). Abiotic stresses reduce the yields of major crops by up to 50% (Francini and Sebastiani, 2015; Sachdev et al., 2021). According to Wang et al. (2013), about 65.8% yield of maize, 82.1% yield of wheat, 69.3% yield of soybeans, and 54.1% yield of potatoes are lost due to these abiotic stresses. Soil salinity and prolonged drought condition are two major stresses among all abiotic stress in this era of global climate change. Under high salinity, plants face nutrient imbalance, reduction in photosynthesis, reduction in photorespiration, and disturbance of iron homeostasis mainly, whereas in case of prolonged drought and heat conditions, usually the seed germination rate, cell division, and photosynthesis rate of plants reduce significantly.

According to the world soil resource report (FAO, 2000), major abiotic stress like drought, cold, and salt affect around 64, 54, and 6% of the entire earth's land, respectively. Approximately 5% of agricultural yield in the primary food-producing nations and roughly 17% yield in other tropical, semi-arid, and desert regions are lost due to these prolonged drought conditions annually (Goswami and Deka, 2019). Besides these major abiotic stresses, extreme temperatures, UV radiation, and heavy metals also significantly reduce crop production worldwide. For each 1 °C increase in mean annual temperature, the yields of wheat, rice, maize, and soybean decreased by 6%, 3.2%, 7.4%, and 3.1% respectively (Zhao et al., 2017).

Nevertheless, biotic stresses also negatively influence crop production globally, about 20–40% of global agronomic produce is annually lost owing to different pests including diseases, insects, weeds, and wild animals (Savary et al., 2012). Various soil-borne fungi, oomycetes, bacteria, and nematodes cause approximately 7–15% crop losses through an array of mechanisms, including the damage of root system, toxins discharge, the production of ROS, reduction in photosynthesis rate, etc (Singh et al., 2019). About 28.2% yield of wheat, 37.4% yield of rice, 31.2% yield of maize, 40.3% yield of potatoes, and 28.8% yield of cotton can be lost globally by these biotic stress agents (Wang et al., 2013).

Several approaches, like plant genetic engineering, chemical control, and the development of stress-resistant varieties, are employed to counter different types of stresses. However, the majority of these strategies are not sustainable, economical, or eco-friendly. The application of beneficial microorganisms as bioinoculants may be a good alternative for promoting plant growth under various types of stresses, especially abiotic stresses. Bioinoculants comprise living or dormant cells of efficient microbial strains that contribute to plant growth by either meeting nutrient requirements or by releasing plant growth hormones or other biological activities like control of pests. In addition to meeting plant's nutritional needs, microbes employed as bioinoculants help to mitigate a range of biotic and abiotic stresses (Benidire et al., 2020). Several mechanisms have been postulated to elucidate how these microbial inoculants

improve plant growth under diverse types of stress conditions by producing different types of biological substances, such as by the production of phytohormones, biofilm, EPS, and ACC deaminase (Ansari et al., 2019; Goswami and Deka, 2019; Tittabutr et al., 2013), production of antioxidants (Singh et al., 2019), cryoprotectants, heat shock proteins, solubilization of minerals like phosphorous (P), potassium (K), and zinc (Zn), nitrogen (N) fixation, and remediation of heavy metals (Jin et al., 2019) through bioaccumulation, biotransformation, and biosorption (Rana et al., 2021); production of siderophore (Ferreira et al., 2019), antibiotics (Jin et al., 2021), hydrolytic enzymes viz. proteases, cellulases, chitinases, and β -glucanases (Veliz et al., 2017), volatile compound (Harun-Or-Rashid and Chung, 2017). Some microbes also enhance induced systematic resistance (ISR) and systemic acquired resistance (SAR) through which they suppress the negative effect of pests (Disi et al., 2019; van Loon, 2007).

Thus, the utilization of bioinoculants may be an economical approach for boosting crop production under multiple stress scenarios. In the present article, the effect of stresses both abiotic or biotic on crop yields, and role of bioinoculants to mitigate these stresses is discussed.

2. Abiotic stresses

Abiotic stress includes extreme temperatures, high salinity, drought or excessive water condition, heavy metals, etc. A large chunk of arable land globally is affected by either of these conditions, which ultimately reduce crop productivity by affecting numerous metabolic processes of the plant.

2.1. Soil salinity and its effect on plant growth and development

Soil salinization is a major environmental issue worldwide, posing detrimental effects on agriculture, and social life in terms of reducing agricultural land usage, limiting agricultural productivity, subsidizing economic returns, etc. According to Sparks (2003), the total salt-affected area worldwide reported 932.2 million ha, of which 37.6% are saline and 62.3% are sodic while according to recent estimation, about 1128 million ha of the area is affected by salt stress globally (Kumar and Sharma, 2020). About 8.2% (76.6 out of 932.2 million ha) salt-affected soil is the result of anthropogenic events, worldwide, for instance, incorrect irrigation, overuse of groundwater, use of chemical fertilizer, and land clearing for cultivation. On the other hand, about 91.8% of salt-affected soil are natural due to eroding of salty parent rock, deposition of fossil salt, and salt carried by rivers and seawater, etc (Kumar and Sharma, 2020).

In salt-affected soils, plants experience two forms of stresses, nutrient stress and osmotic stress (Ashrafi et al., 2014). When an excess aggregate of Na^+ and Cl^- ions are present in the soil, it reduces the osmotic potential of soil, due to which plants can't absorb enough water and nutrient, and experience osmotic stress. Salinity-stressed plants face either toxicity of nutrients such as sodium (Na), boron (B), and chlorine (Cl), or deficiency of essential nutrients such as N, P, K, Fe, etc. In saline soils, N uptake is inhibited as a result of high concentrations of Cl^- & Na^+ ions and water uptake, Cl^- ions interact with NO_3^- and Na^+ ions interact with NH_4^+ . According to Bano and Fatima (2020) & Shrivastava and Kumar (2015), P uptake by the plant is also reduced since $(\text{PO}_4)^{3-}$ ion precipitate with Ca^{2+} ions and form calcium phosphate. On the other hand, increased concentration of Na^+ ions, reduce K^+ ion absorption rapidly (Raddatz et al., 2020). In sodic conditions, Ca^{2+} uptake was also reduced. Ca^{2+} and Mg^{2+} compete with each other during the uptake process in the plant, in high Ca^{2+} concentrations plants face Mg^{2+} deficiency and vice versa (Parihar et al., 2015).

In saline soils at high pH, plants experience deficiency of cationic micronutrients and face toxic effects of some anionic micronutrients. Among the micronutrients, B toxicity and Zn deficiency problem has been reported worldwide in saline soil. Some plants absorb molybdenum (Mo) and selenium (Se) in higher concentrations in an anionic form in

saline soil that may be harmful to the animals eating such plants (Qadir and Schubert, 2002).

High salinity is also responsible for the generation of ROS that causes per-oxidation of lipids, inactivation of enzyme or protein, etc. The major sites of ROS formation are the electron transport chain in mitochondria and the chloroplast (Hasanuzzaman et al., 2020). Inhibition of CO₂ fixation due to stomata closure leads to increased excitation energy in chloroplast which generates free oxygen radicals (Ahmad et al., 2010). According to Abd Elgawad et al. (2016) increased NaCl concentration induces oxidative stress in *Zea mays* (maize) roots and mature leaves. A recent study reports that the stability of DNA is also reduced by ROS generated under high NaCl concentrations. Single-strand breaks in DNA occur through hydroxyl radical and double-strand break-induced by programmed cell death in moss *Physcomitrella patens* (Zvanarou et al., 2020). Chlorotic toxicity occurs due to high Cl⁻ ions concentration that leads to chlorophyll reduction, in contrast, a high concentration of Na⁺ ions disturb the stomatal function by reducing K uptake in leaves (Parihar et al., 2015).

High salinity reduces seed germination in *Posidonia* (Torquemada and Sánchez Lizaso, 2013), *Zea mays* (Khodarahmpour et al., 2012), and *Glycine max* (soybean) (Zuffo et al., 2020) were reported recently. Salinity affects germination by reducing water uptake by seeds due to less osmotic potential that decreases seed reserve utilization (Othman et al., 2006), alters the activities of enzymes (Gomes-Filho et al., 2008), and interrupts hormonal homeostasis (Shahid et al., 2020).

2.1.1. Salinity stress tolerance induced by different types of bioinoculants

Several microbes inhabiting the plant microbiome including the rhizosphere have the potential to mitigate the salinity stress by producing different compounds such as phytohormones-like auxin, gibberellin, cytokinin (CK), enzymes like ACC deaminase, extracellular polymeric substance, volatile compound, production of siderophore, biofilm formation, production of osmolytes, or by enhancing antioxidant production (Figure 1). Microbes also boost plant growth by augmenting nutrient

availability by N fixation, P & K solubilization, etc., under saline conditions.

Salinity induces, rapid synthesis of ethylene which is harmful and inhibits plant growth but in normal conditions ethylene hormone plays many important roles including seed germination, root development, fruit ripening, leaf abscission, etc. Some microbes produce ACC deaminase that breaks the precursor of ethylene, ACC into ammonia & α-ketobutyrate and regulates ethylene concentrations in plants (Chatterjee et al., 2018), and maintains the plant growth in saline conditions (Moon and Ali, 2022; Ansari et al., 2019; Mishra et al., 2018). Numerous studies have shown that the ACC deaminase secreting microbes strengthen plant development in saline environments such as *Microbacterium oleovorans* and *Rhizobium massiliae* in *Capsicum annuum* (pepper) (Hahm et al., 2017), *Bacillus pumilus* in *Zea mays* (maize) (Mukhtar et al., 2020), *Bacillus cereus* in *Vigna radiata* (mung bean) (Islam et al., 2016), *Azotobacter salinestris* in *Sorghum bicolor* (sorghum) (Omer et al., 2016), *Bacillus pumilus* in *Oryza sativa* (rice) (Kumar et al., 2020; Khan et al., 2016) and *Enterobacter* strain G in *C. cajan* (Anand et al., 2021).

Some microbes produce and also enhance the endogenous production of abscisic acid (ABA) in plants (Forni et al., 2017; Goswami and Deka, 2020). ABA upregulates during water deficiency in saline conditions, that helps the plant to control stress impact. ABA also helps plant roots to synthesize compatible solutes like proline, sugar, and K⁺ ions as well which alleviate salinity effects (Kumar and Sharma, 2020). Auxin, gibberellin, and cytokine are other important hormones that are produced by different microorganisms such as *Nostoc kihlmani*, *Anabaena cylindrical* (Gheda and Ahmed, 2015), *Bacillus mojaviensis*, *Pseudomonas fluorescens* (Metoui Ben Mahmoud et al., 2020) that enhance the plant growth under such conditions. Recent reports suggest that the casparian bands are important for salt tolerance. Bacterium-induced hormone production accelerates the formation of casparian bands and ion homeostasis in salt-stressed plants (Martynenko et al., 2022).

Likewise, many microbes produce biopolymers and osmolytes and also induce the formation of antioxidant enzymes. Biopolymers like EPS

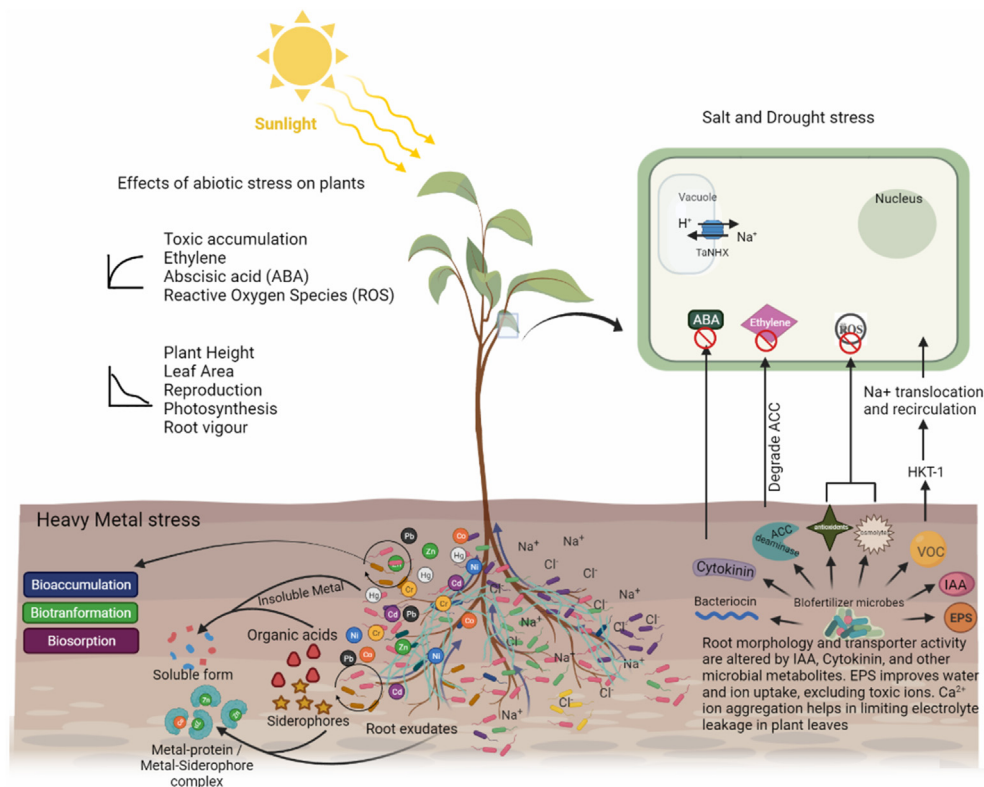


Figure 1. Mechanisms for the amelioration of abiotic stress and plant growth promotion induced by microbes.

play a significant role in mitigating salinity stress by binding with cations like Na^+ and reducing its availability, which helps in increasing water potential and nutrient uptake. Several findings suggest that EPS-producing microbial inoculants with a variety of plant growth-promoting properties reduce salt stress in crops and have a positive outcome on plant and soil conditions (Table 1). *Bacillus licheniformis* mitigate salinity stressors in *Triticum aestivum* (wheat) by the production of EPS along with nitrogen fixation and ACC deaminase activity (Singh and Jha, 2016). Microbially induced osmolytes and antioxidants are also reported in various studies, for instance, *Bacillus cereus* and *Streptomyces* strains enhanced *Vigna radiata* (mung bean) and *Triticum aestivum* (wheat) growth in saline conditions due to amplified antioxidant enzymes, respectively (Akbari et al., 2020; Islam et al., 2016). Osmolytes such as sugar, glucosyl glycerol, amino acids, and betaines are accumulated by the plants which aid in resistance to salinity stress by sustaining the osmotic balance of the cell (Kumar et al., 2020).

Microbes also play a pivotal function in fulfilling the essential nutrient requirements of the plant in a saline environment. Under saline conditions, the competence of a plant to uptake or store nutrients is

reduced rapidly. Microbes enhance plants growth by nutrient uptake or accumulation rate like *Nostoc kihlmani*, *Anabaena cylindrical* increase nitrogen fixation in *Triticum aestivum* (Gheda and Ahmed, 2015). Similarly, *B. megaterium* enhances P solubilization by chelation or acidification and enhance the growth of *Phaseolus vulgaris* (Abdelmoteleb and Gonzalez-Mendoza, 2020). Under saline conditions, K solubilizing microbes perform a vital role to fulfill the K requirement of the plant. An investigation by Jan et al. (2018) disclosed increased K & P solubilization by *Gloeocapsa* sp. that enhances the growth of *Oryza sativa* (rice) plants.

Deficiency of Fe under saline environment is also a common problem that plants face. Microorganisms help in Fe supply by two possible mechanisms, first by supplying the iron from soil chelated by microbial siderophore (Krohling et al., 2016) and secondly by exchanging Fe(II) with phytosiderophore that reduce microbial siderophore to donate Fe(II) to the plant transport system due to high redox potential (Ahmed and Holmström, 2014). A study by Kumar et al. (2017) revealed that *Oryza sativa* seedling, germination rate, and shoot length were enhanced significantly by siderophore producing *Pseudomonas aeruginosa*. In a recent finding by Ali et al. (2022), inoculation of *Enterobacter cloacae*

Table 1. Effects of different microbial inoculants in the alleviation of salinity stress and enhancement of stress tolerance in plants.

Bioinoculants	Plants	PGP attributes	Effect on plants growth and soil condition	Reference
<i>Pseudomonas fluorescens</i> , <i>Pseudomonas putida</i> , and <i>Bacillus subtilis</i>	<i>Vicia faba</i>	Increased Proline content	Fresh weight (root & shoot), Plant height, and leaf area significantly enhanced	Metwali et al. (2015)
<i>Microbacterium oleivorans</i> , <i>Rhizobium massiliense</i>	<i>Capsicum annuum</i>	IAA, ACC deaminase and siderophore production	Plant height, weight, and chlorophyll contents significantly enhanced	Hahm et al. (2017)
<i>Kocuria rhizophila</i>	<i>Zea mays</i>	IAA production and P solubilization and regulate ABA levels	Enhanced seed germination, photosynthetic capacity, biomass & antioxidant levels, relative water content	Li et al. (2020)
<i>Bacillus megaterium</i>	<i>Phaseolus vulgaris</i>	P solubilization	Enhanced plant growth, phosphate uptake, and photosynthetic pigments	Abdelmoteleb and Gonzalez-Mendoza (2020)
<i>Glomus mosseae</i> and <i>Sinorhizobium meliloti</i>	<i>Medicago sativa</i>	Increased N, P, and proline content in shoot	Enhanced yield, mycorrhizal infection, nodule weight, and number and	Ashrafi et al. (2014)
<i>Bacillus subtilis</i> and AMF (<i>Claroidoglomus etunicatum</i> , <i>Rhizophagus intraradices</i> , <i>Funneliformis mosseae</i>)	<i>Acacia gerrardii</i>	Increased levels of glycine, proline, betaine, and α -amino acids and enhanced Na/K ratio	Enhanced biomass (shoot and root weight), nodule number, stomatal conductance, and leghemoglobin quantity	Hashem et al. (2016)
<i>Bacillus pumilus</i>	<i>Zea mays</i>	IAA, ACC deaminase activity, P-solubilization, EPS production and higher osmoprotectants and malondialdehyde production	Enhanced root and shoot dry weights	Mukhtar et al. (2020)
<i>Bacillus cereus</i>	<i>Vigna radiata</i>	IAA, ACC deaminase, antioxidant enzymes and enhanced the accumulation of proline, potassium, nitrogen, and phosphorus	Enhanced fresh and dry biomass, plant height, and yield.	Islam et al. (2016)
<i>Anabaena cylindrical</i> , <i>Nostoc kihlmani</i>	<i>Triticum aestivum</i>	IAA, CK, GA, and EPS production	Enhanced the Physico-chemical quality of soil and improved soil health and plant growth	Gheda and Ahmed (2015)
<i>Gloeocapsa</i> sp.	<i>Oryza sativa</i>	N fixation, P and K solubilization	Enhanced the soil organic matter, and plant dry weight	Jan et al. (2018)
<i>Nostoc ellipsosporum</i> and <i>Nostoc punctiforme</i>	<i>Triticum aestivum</i>	N fixation and P solubilization	Enhanced Improved soil physical structure, nutrient status, and microbial activity	Nisha et al. (2018)
<i>Pseudomonas aeruginosa</i>	<i>Oryza sativa</i>	P solubilization, siderophore	Enhanced the growth of seedling (germination percentage, plant length)	Kumar et al. (2017)
<i>Jeotgalicoccus huakuui</i>	<i>Zea mays</i>	IAA, ACC deaminase, biofilm formation	Enhancement of all vegetative parameters and total yield	Misra et al. (2019)
<i>Azotobacter salinestris</i>	<i>Sorghum bicolor</i>	Enhanced ACC deaminase, salicylic acid, proline, and EPS production	Significant increase in growth parameters, chlorophyll, total carbohydrate, proline, and macro-elements content	Omer et al. (2016)
<i>Virgibacillus marismortui</i> , <i>Alkalibacillus haloalkaliphilus</i>	<i>Triticum aestivum</i>	IAA, ACC deaminase activity, siderophore	Enhanced total fresh weight of shoots, ears, and stems about two times, and more the grain yield about 15%	Torbaghan et al. (2017)
<i>Bacillus licheniformis</i>	<i>Triticum aestivum</i>	IAA, ACC deaminase activity, P-solubilization, proline aggregation, EPS production and N fixation activity	Enhanced plant growth in terms of plant height, fresh, and dry weight	Singh and Jha (2016)
<i>Hartmannbacter diazotrophicus</i> and <i>Pseudomonas</i> sp.	<i>Medicago sativa</i>	Higher membrane stability index with reduced Na^+ conc. in plant cells	Enhanced the root length and weight, nodule number, chlorophyll content	Ansari et al. (2019)
<i>Bacillus pumilus</i>	<i>Oryza sativa</i>	IAA, ACC deaminase, P-solubilization, proline aggregation, and EPS production	Enhanced plant height, plant fresh, & dry weight, chlorophyll & carotenoids content	Khan et al. (2016); Kumar et al. (2020)
<i>Bacillus mojavensis</i> , <i>Pseudomonas fluorescens</i>	<i>Hordeum vulgare</i>	Enhanced IAA and proline production	Enhanced water and nutrient uptake and stimulate root development	Metoui Ben Mahmoud et al. (2020)

PM23, significantly enhanced maize growth under saline condition due to indole-3-acetic acid (IAA), ACC deaminase, siderophore, exopolysaccharides etc.

2.2. Drought stress and its effects on plant growth and development

Worldwide, about half of the terrestrial surface, including most of the agricultural lands, is affected by drought. Growing population, intensive agriculture, and expanding industrial sector are some of the major reasons for water scarcity besides climate change. According to Goswami and Deka (2019) during the period from 1970 to 2000, the drought-affected area increased more than twice the rate, and by 2050 it is expected to affect half of the land worldwide.

A high rate of transpiration and very low moisture content in soil are the main factors that induce drought stress in the plant. Drought conditions affect all stages of plant life and their metabolic and physiological activities like membrane integrity, photosynthesis, pigment content, growth, and yield, etc. Drought reduces photosynthesis significantly mainly by disrupting major components of photosynthesis such as stomatal control, electron transport chain of thylakoid, chloroplast lipids, and pigment & protein content (Anjum et al., 2011). Likewise, in such conditions, ABA concentration also increases in the leaf which enhances K^+ efflux from guard cells of stomata. Due to the efflux of K^+ in the guard cell, turgor pressure decreases rapidly which closes stomata, which decreases the photosynthesis rate (Anjum et al., 2011). In the case of severe drought conditions, the activity of RuBisCO is also reduced in many plants (Kaur and Asthir, 2017). Seed germination and stand establishment are very poor during drought conditions. During water stress, enough water is not available for seed, which reduces seed germination and plant number per unit area.

Drought interrupts water drift towards meristematic cells that inhibit cell elongation severely. Leaf size and the number of leaves also decrease due to low turgor pressure and a reduction in photosynthesis in water deficit events (Anjum et al., 2011; Zia et al., 2021). Flower production and grain filling are also negatively affected by drought stress, reducing the size and number of grains that reduce crop yield significantly. Zhang et al. (2018) analyzed rice and wheat yield databases, which showed about 27.5% yield of wheat and 25.4% yield of rice decreased under drought stress conditions. Another recent meta-analysis study on 120 published case studies showed that the yield of crops decreases under drought, water, and heat stress (Cohen et al., 2021). The nutritional value and quality of seeds mainly the protein and antioxidant compounds increase under stress conditions while the carbohydrate and lipid decrease (Zia et al., 2021).

2.2.1. Drought stress mitigation using bioinoculants

Microorganisms secrete various phytohormones, EPS, antioxidants, and osmolytes, etc., that play an important role in increasing drought tolerance during water deficit conditions. Phytohormones like ABA, IAA, CK have an important role in drought stress mitigation. Auxin regulates several functions in plant cell such as differentiation of vascular tissue, root initiation, cell division, and elongation, etc. Auxins play a vital role in root growth and architecture. Prolonged stress conditions result in reduced endogenous IAA levels, which restrict plant growth. Auxin-producing microbes can enhance endogenous IAA synthesis and improve plant development in drought events (Goswami and Deka, 2020). Additionally, research suggests that bacterial IAA promotes the production of ACC deaminase, which dissociates one of the ethylene precursors and delays the onset of senescence in stressed plants (Uzma et al., 2022). Like auxin, CK is another plant hormone that is important in preventing early leaf mortality in water-deficit conditions. Microbes can increase the synthesis of the endogenous stress hormone ABA, which is critical for the plant's drought resistance. A higher level of endogenous ABA upregulates the hydraulic conductivity of roots and on the other hand, ABA also upregulates aquaporins (Goswami and Deka, 2020). Under stress conditions, microbially produced ACC deaminase resists

plant root drying by degrading ACC and reducing the level of ethylene in the plant cell (Ngumbi and Kloepper, 2016). Murali et al. (2021) reported that, treating *Pennisetum glaucum* with *Bacillus amyloliquefaciens* (MMR04) significantly decreased the comparative expression of DREB-1E (drought-responsive) and ERF-1B (ethylene-responsive) genes in *Pennisetum glaucum*.

A signalling molecule, salicylic acid production is enhanced endogenously by several microorganisms in the plant that play an important role in the regulation of plant growth by inducing the number of gene expressions that function as antioxidants, heat shock proteins, and secondary metabolites in stress conditions (Islam et al., 2020).

Under stress conditions, microbial osmolytes work with plant osmolytes, like proline, mannitol, sucrose, glycine betaine, etc., to maintain turgor pressure and increase the water potential of the plant cell (Ma et al., 2020). Proline has been considered the most important osmolyte that also acts as a metal chelator and antioxidant. Another osmoprotectant, trehalose stabilizes dehydrated enzymes and plant membrane thus enhancing the osmoprotection in the plant (Goswami and Deka, 2020). Likewise, EPS protect the plant from desiccation by increasing root tissue and adhering soil ratio (Morcillo and Manzanera, 2021).

Microbial inoculation also enhances the synthesis of antioxidant enzymes in the plant, which helps the plant to enhance drought tolerance by reducing ROS and enhancing the production of antioxidant enzyme. A report by Batool et al. (2020) showed that inoculating potatoes with *Bacillus subtilis* HAS31 reduced ROS production and monodehydroascorbate (MDA) production while increasing catalase, peroxidase, superoxide dismutase, and total soluble sugar in drought-stressed environments.

A current finding from Singh et al. (2020) showed that the microbial inoculation of *Trichoderma* and *Pseudomonas* enhances the growth of *Oryza sativa* (rice) by the production of antioxidant enzymes such as peroxidase, glutathione peroxidase, ascorbate peroxidase, and glutathione reductase under drought conditions. Bioinoculants elicit pathways and molecules to alleviate drought stress in crops (Figure 1). Table 2 summarises reports showing positive outcomes for plant growth and soil conditions.

2.3. Temperature stress & its effects on plant growth and development of plant

Various growth stages of plants, from seed germination to reproduction, are affected by heat stress at physical, physiological, and biochemical levels. During high-temperature stress, seed germination rate and stand establishment are reduced due to the disturbed activity of enzymes involved in the breakdown of starch and synthesis of ABA & GA (Begcy et al., 2018). The process of photosynthesis is severely influenced by high temperatures due to disorganization of thylakoid, swelling & loss of grana, a decline in the activity of electron acceptor & donor sites of photo-system (PS) II, and reduction in the activity of enzymes like RuBisCO (Hassan et al., 2020). Besides, heat stress also reduces photosynthesis by affecting intercellular CO_2 concentration due to stomata closure and by loss of chlorophyll pigment due to lipid peroxidation of chloroplast (Hassan et al., 2020).

Heat stress also reduces plant growth by affecting the relative water content of plant and nutrient uptake by increasing evapotranspiration and reducing root growth as well as water uptake. A research by Giri et al. (2017) revealed that the biomass of root decreased significantly which reduced the nutrient uptake, protein assimilation, and the total protein content of *Solanum lycopersicum* root under severe heat stress. Reduction of relative water content and photosynthesis rate alters the osmotic adjustment of the plant. Relative water content and leaf area are also reduced by heat stress in *Brassica campestris* (Zou et al., 2016). Additionally, like other abiotic stresses, heat stress induces the synthesis of ROS mainly in chloroplast, mitochondria, and peroxisome. According to studies, excessive ROS can cause oxidation of proteins, lipids, DNA damage, and cell death (Medina et al., 2021). Overall, heat stress

Table 2. Effects of different microbes as bioinoculants in the alleviation of drought stress and enhancement of stress tolerance in plants.

Bioinoculants	Plants	PGP attributes	Effect on plants growth and soil condition	Reference
<i>Pseudomonas putida</i>	<i>Cicer arietinum</i>	ROS scavenging with higher SOD or catalase	The germination rate, root length and number of lateral roots increased	Tiwari et al. (2016)
<i>Rhizophagus irregularis</i>	<i>Glycyrrhiza uralensis</i>	Higher Chl a and Chl b, and C:N ratios, improved photosynthetic rate & stomatal conductance	Nodulation, plant shoot and root phosphorus & nitrogen contents increased, accumulation of glycyrrhizin and liquiritin	Hao et al. (2019)
<i>Bacillus megaterium</i>	<i>Triticum aestivum</i>	Enhanced production of osmolytes	Enhanced plant biomass, photosynthetic pigments, and relative water content	Rashid et al. (2021)
<i>Streptomyces chromofuscus</i> , <i>Streptomyces ambofaciens</i> , and <i>Streptomyces gardneri</i>	<i>Helianthus</i> sp.	Enhanced IAA and ACC deaminase	Increased the germination, radicle and hypocotyl length	Zahra and Hamed (2020)
<i>Glomus mosseae</i> , <i>Sinorhizobium meliloti</i>	<i>Medicago sativa</i>	Increased proline content	Enhanced membrane stability and osmotic potential. Higher photosynthetic indices, and forage yield	Zafari et al. (2017)
<i>Klebsiella</i> sp.	<i>Triticum aestivum</i>	Increased proline content	Enhanced biometric parameters, photosynthetic indices, osmotic potential, and membrane stability	Gontia-Mishra et al. (2016)
<i>Bacillus pumilus</i>	<i>Zea mays</i>	ABA, IAA, and GA increased	Increased osmotic potential, chlorophyll, protein and water content,	Yasmin et al. (2017)
<i>Azotobacter</i> sp. <i>Azospirillum</i> sp. <i>Glomus mosseae</i>	<i>Sorghum bicolor</i>	Increased IAA, total anthocyanin, carotenoid and flavonoid content, antioxidant enzyme activity	Improved the chlorophyll, soluble proteins, proline content. Grain yield, panicle length, was enhanced and the electrolyte leakage decreased	Kamali and Mehraban (2020)
<i>Bacillus amyloliquefaciens</i>	<i>Lycopersicon esculentum</i>	Higher IAA, ACCD and EPS production	Germination rate, plant height, and dry biomass, the photosynthetic potential was enhanced significantly and the leaf temperature was reduced	Astorga-Eló et al. (2021); Eke et al. (2019)
<i>Pseudomonas aeruginosa</i>	<i>Vigna radiata</i>	ACC, IAA, Proline, P- solubilization, siderophore production	Enhanced dry biomass, production of ROS scavenging enzymes, and upregulation of dehydration responsive element binding protein, catalase, and dehydrin genes	Sarma and Saikia (2013)
<i>Azospirillum brasilense</i> and <i>Stenotrophomonas maltophilia</i>	<i>Triticum aestivum</i>	Increased Chl a & b, ascorbic acid, lowered proline conc. electrolyte leakage, malondialdehyde and H ₂ O ₂ accumulation	Enhanced chlorophyll content, and water use efficiency. Better grain yield	Kasim et al. (2021)
<i>Piriformospora indica</i>	<i>Glycine max</i>	Increased N, P, and K content in shoot, upregulation of iron scavenging, ABA, auxin, and GA ₃ synthesis genes	Enhanced root length and volume, chlorophyll contents, and relative water content	Bajaj et al. (2018)
<i>Rhizobium</i> sp.	<i>Arachis hypogaea</i>	Higher ACC, EPS and IAA production, increased Fe and P availability	Enhanced germination, plant weight, nutrient content, drought tolerance and yield	Igiehon et al. (2019)
<i>Xerocomus badius</i>	<i>Lolium multiflorum</i>	Not presented	Enhanced germination rate and seedling growth	Liu et al. (2021)
<i>Pseudomonas azotoformans</i>	<i>Triticum aestivum</i>	IAA, ACC deaminase, P- solubilization, EPS production	Enhanced photosynthetic pigment, antioxidative enzymatic activity and overall plant growth	Ansari et al. (2021)

conditions negatively affect all stages of plant life and ultimately reduce crop yield.

Low-temperature stress also has deleterious effects on plant growth, especially in temperate and high-elevated regions worldwide. Low temperature, during the early stages, is responsible for reduced plant growth, discoloration of the leaf, and transplanted seedling mortality (Arun-Chinnappa et al., 2017). The sterility of pollen is also induced by low temperature mainly due to degradation of starch granules, inhibition of germination, and reduction in tube elongation (Shinada et al., 2013). In addition to damage of different cellular components, low temperature also reduces the photosynthesis process by altering the chlorophyll and thylakoid organization (F Zhang et al., 2020). The primary site of freezing injury in the plant is the membrane system (Waraich et al., 2012). Freezing stress induce cellular dehydration in leaf cell due to ice formation in the apoplast which induces stomatal closure and alters cellular homeostasis, whereas in the case of root, low-temperature stress induces cellular dehydration, which is induced due to water imbalance in the cell (Arun-Chinnappa et al., 2017). Freezing stress also induces cell break due to formation of stress-induced ROS which degrade the cell membrane because ice formation occurs within the cell wall and membranes leading to cell rupture (Waraich et al., 2012).

2.3.1. Temperature stress tolerance induced by different bioinoculants

Several microbes which are used as bioinoculants can survive very high and very low temperatures by employing strategies like formation of heat shock protein, biofilm formation, production of osmo-protective compounds (Bruno et al., 2020), formation of cold-shock proteins,

cryoprotectants, ice nucleation factors, etc. (Mishra et al., 2011), and by enhancing plant growth by producing phytohormone, siderophores production and mineral solubilization. A recent finding by Khan et al. (2020) confirmed that the application of thermotolerant *B. cereus* SA1 enhances soybean growth significantly under heat stress by increasing the production of antioxidants and reduction of ABA concentration in inoculated plants. Under high temperature and freezing stress, synthesis and influx of osmolytes like amino acids (proline), sugars, polyamine, quaternary amine (glycine betaine) increases as these osmolytes play a vital role in protecting and neutralizing the effect of stress and maintaining cellular homeostasis (Jogawat, 2019). Some studies showed that the increased proline accumulation enhances inhibitory consequences during high-temperature stress but in other stress conditions such as freezing and other osmotic stress accumulation of proline plays a vital role in heat stress alleviation (Lv et al., 2011) (Table 3). Priming with *Bacillus safensis* induces heat stress tolerance in *Triticum aestivum* (wheat) seedling by reducing ROS production thus minimizing membrane and chloroplast damage. This study also shows that the concentration of proline reduced and the concentration of glycine betaine increased in inoculated wheat during stress conditions (Sarkar et al., 2018).

Nevertheless, some study also demonstrates the ability of microbial inoculation in enhancing cold tolerance in plants. Inoculation of *Rhizophagus irregularis* enhances photosynthetic efficiency, sugar level, and non-photochemical quenching in *Cucumis sativus* (cucumber) (Ma et al., 2019). Similarly, inoculation of *Trichoderma* sp., *Pseudomonas vancouverensis*, and *P. fredericksbergensis* enhanced photosynthesis and growth rate by reducing lipid peroxidation, electrolyte leakage, reducing ROS

Table 3. Effects of application of bioinoculants on the plant growth and alleviation of temperature stress.

Bioinoculants	Plants	Effect on plants	Stress type	Reference
<i>Bacillus cereus</i>	<i>Solanum lycopersicum</i>	Enhanced plant biomass, chlorophyll content, and chlorophyll fluorescence	Heat	Khan et al. (2020)
<i>Providencia rettgeri</i>	<i>Sorghum bicolor</i>	Enhanced fresh & dry weight, down-regulation of the proline synthesizing genes. Increased expression of sod, apx1, and cat, and (sHsp) genes	Heat	Bruno et al. (2020)
<i>Bacillus amyloliquefaciens</i>	<i>Triticum aestivum</i>	Enhanced plant survival rate, reduced expression of stress related genes	Heat	Abd El-Daim et al. (2014)
<i>Bacillus safensis</i>	<i>Triticum aestivum</i>	Reduced ROS accumulation	Heat	Sarkar et al. (2018)
<i>Rhizophagus irregularis</i>	<i>Vigna unguiculata</i>	Enhanced root biomass and chlorophyll content	Cold	Ma et al. (2019)
<i>Trichoderma harzianum</i>	<i>Solanum lycopersicum</i>	Enhanced fresh and dry weights, and proline accumulation	Cold	Ghorbanpour et al. (2018)
<i>Bacillus amyloliquefaciens</i> , <i>Brevibacillus laterosporus</i>	<i>Oryza sativa</i>	Enhanced proline, chlorophyll and overall plant growth. Decreased leaf MDA content and electrolyte leakage	Cold	Kakar et al. (2015)
<i>Pseudomonas vancouverensis</i> and <i>Pseudomonas fredericksbergensis</i>	<i>Solanum lycopersicum</i>	Reduced ROS concentration, membrane damage and Improved plant growth, and robustness	Cold	Subramanian et al. (2015)
<i>Lysinibacillus fusiformis</i> YJ4 and <i>Lysinibacillus sphaericus</i> YJ5	<i>Zea mays</i>	Enhanced plant growth, total phenolic content, osmolytes, antioxidant enzyme, and phytohormones levels	Cold	Jha et al. (2022)

concentration, increasing leaf water and proline concentration in *Solanum lycopersicum* (tomato) under cold stress (Ghorbanpour et al., 2018; Subramanian et al., 2015). Another research conducted by Kakar et al. (2015) demonstrated that cold stress tolerance of the *Oryza sativa* (rice) plant enhanced by the inoculation of *Bacillus amyloliquefaciens* and *Brevibacillus laterosporus*. The concentration of MDA and electrolyte leakage decreased, and the aggregation of proline and chlorophyll content increased in the inoculated plants. Inoculation of cold-tolerant *Lysinibacillus fusiformis* YJ4 and *Lysinibacillus sphaericus* YJ5 strains increased total phenolic content, osmolytes, antioxidant enzyme, and phytohormones levels in maize significantly (Jha et al., 2022).

2.4. Flood stress in plants and its mitigation using bioinoculants

Flooding or submergence causes anoxia, which affects around 15 million hectares of Asia's rain fed territory and approximately 13% of the

earth's total agriculture land (Meena et al., 2017; Neeraja et al., 2007). Hypoxic environments diminish the levels of endogenous plant hormones such as IAA, GA, and CK, resulting in accumulation of ABA and ethylene in shoots, causing early senescence (Glick, 2014) and triggering the production of ROS, which provokes irreversible harm to the plant under stress (Blokchina and Fagerstedt, 2010; Meena et al., 2017). On the other hand, the enzyme ACC synthase, which is responsible for the conversion of S-adenosyl-L-methionine (SAM) to ACC, is significantly increased in plant roots, where, hypoxia prevents the freshly generated ACC from being oxidised and delivered to the shoot, resulting in chlorosis, necrosis, and reduced productivity (Ali and Kim, 2018; Glick et al., 2007; Paul et al., 2016). ACC deaminase-producing bioinoculants can help to reduce ACC and ethylene concentrations by 2 to 4-fold and attenuate the negative impacts of waterlogging stress (Ali and Kim, 2018; Grichko and Glick, 2001a). According to Ali and Kim (2018), *S. indicum* treated with the ACC deaminase-producing rhizobacteria *Pseudomonas veronii* had a positive impact on alleviating waterlogging stress-related damage by improving chlorophyll content and plant biomass. Similarly, Barnawal et al. (2012), found that *Ocimum sanctum* inoculated with *Achromobacter xylosoxidans*, *Herbaspirillum seropedicae*, *Serratia ureilytica*, and *Ochrobactrum rhizosphaerae* yielded 46.5% more than uninoculated stressed plants in waterlogged conditions. Efficacy of various *Pseudomonas* sp. strains in alleviating hypoxic conditions in *Cucumis sativus*, *Lycopersicon esculentum*, and *Brassica napus* has also been documented (Farwell et al., 2007; Grichko and Glick, 2001b; Li et al., 2013). Nascimento et al. (2012) modified *Mesorhizobium ciceri* with an exogenous ACC deaminase gene from *Pseudomonas putida* and observed high growth promotion and nodulation capabilities in chickpea under stress conditions.

2.5. Heavy metals and their impact on plant growth and development

Heavy metals such as Cobalt (Co), Copper (Cu), Chromium (Cr), Manganese (Mn), Iron (Fe), Cadmium (Cd), Mercury (Hg), Arsenic (As), Nickel (Ni), Zinc (Zn), and Lead (Pb) are natural constituents of the ecosystem but above the threshold value, they are toxic for living organisms. Increasing heavy metals contamination in soil and water is a major problem around the world, because of their non-degradable and toxic nature. The source of heavy metals in the environment can be natural processes like a volcanic eruption, weathering of rock, soil erosion, etc., or anthropogenic like increasing industrialization, intensive agriculture, and urbanization (Kurniawan et al., 2022; Ayangbenro and Babalola, 2017).

Plant requires many heavy metals for their growth and development; however, an excessive number of heavy metals can be toxic for the plant. Plants absorb these heavy metals from the contaminated soil solution, disposition of excessive amount of these metals within the plant adversely affect the plant growth either directly by inhibition of cytoplasmic enzyme activity and oxidative stress etc., or indirectly by altering plant-microbe interaction and by reducing the absorption of the essential minerals from the soil (Dotaniya and Saha, 2016). Heavy metals are also toxic to beneficial soil microorganisms and the fertility level of soil reduces continuously due to the reduction of beneficial soil microbes, which ultimately influences the growth of plants (Dotaniya and Saha, 2016).

Heavy metals including Pb, Hg, Cd, As do not play any beneficial role in plants growth however, they are very toxic to plants even in minute concentration (Chibuikwe and Obiora, 2014). Besides these non-essential heavy metals, and some essential heavy metals like Cu, Ni, Co, Fe, Mn also can be toxic to plant at high concentrations (Chibuikwe and Obiora, 2014).

2.5.1. Heavy metal stress tolerance as induced by different types of bioinoculants

Modern agricultural practices are the main region of heavy metals contamination in agricultural soil which includes chemical fertilizers,

pesticides, sewage sludge, irrigation waters, liming, etc (Alengebawey et al., 2021). Heavy metals can be managed by either physiochemical or biological techniques. Physiochemical methods are challenging due to the high cost, complicated technical requirements, and creation of secondary pollutants. Conversely, biological methods are organic, eco-friendly, and economical (Tiwari and Lata, 2018). The use of microbial inoculants is one such biological approach that not only aids in the development of the healthy crop but also facilitates the immobilization or detoxification of toxic heavy metals from the infested soils (Jhilta et al., 2021). Microorganisms have several advanced mechanisms to tolerate heavy metals like hauling metals and metal ions across the cytoplasmic barrier, biosorption & bioaccumulation, precipitation, and detoxification via a redox reaction (Kurniawan et al., 2022; Rana et al., 2021; Tiwari and Lata, 2018) (Figure 1). These microbes alter or reduce the bioavailability of heavy metals for the plant by the process of acidification, precipitation, and chelation. Several microorganisms produce organic acids that chelate heavy metals (Seneviratne et al., 2017) which is a key component in heavy metal solubilization (Mishra et al., 2017). Many other compounds such as EPS, siderophores, and growth hormones are also synthesized by different microbes which facilitate detoxification of heavy metals by biosorption or bioaccumulation and promote plant growth in contaminated soil (Table 4).

Microbial EPS have anionic functional groups that bind heavy metals through proton exchange and micro-precipitation. EPS also induces biofilm formation, which helps in the detoxification of heavy metals (Mishra et al., 2017). Microbial siderophores are also significant in metal chelation. Additionally, phytohormones produced by microbes can counter heavy metal toxicity by enhancing the antioxidative enzymes in the plant (Nazli et al., 2020). Heavy metal tolerant (HMT) plant growth-promoting bacteria (PGPB) not only reduce the toxic effect of

heavy metals but also promote growth in plants under such environments. Inoculation of the HMT-PGPB consortium not only reduces the bioavailability of heavy metals (Cu, Cd, Pb, Zn) but also enhances sorghum bicolor plant growth (El-Meihy et al., 2019). Similarly, inoculation of *Enterobacter* sp. with biochar and gravel sand reduces Cd bioavailability and enhances *Pisum sativum* growth significantly (Naveed et al., 2020). The inoculation of *Klebsiella pneumoniae*, *Bacillus pumilus*, *Klebsiella* sp., *Enterobacter* sp., and *Mucor* sp., also reduce heavy metals contamination significantly and enhances plant growth (Ahmad et al., 2015; Karthik et al., 2016; Ma et al., 2015; Mitra et al., 2018; Pramanik et al., 2017; Zahoor et al., 2017).

Hu and Zhao (2007) studied the amelioration of Ni, Co, Cd, Cu by *P. putida* CD2 and reported that heavy metal resistance may have arisen as a result of the activation of cadmium-resistant traits, which comprised five *czc* operons and two *cadA* genes. Energy-dependent efflux processes involving CBA-type chemiosmotic antiporters, P-type ATPases, and cation diffusion facilitators (CDF) were also implicated in heavy metal tolerance.

3. Biotic stresses

Plants interact with several living organisms, both beneficial and harmful. About 20–40% of global crop production is annually lost due to the infection of pathogens, herbivory, and weeds. Infestation of crops by different organisms like insects, mites, snails, slugs, and bugs, has a drastic effect on the crop. Several physical and metabolic changes occur in the host due to herbivory invasion such as changes in CO₂ assimilation, reduction in nutrients and reduced photosynthesis in affected leaf, increased water loss (Peschiutta et al., 2018), which ultimately reduce the growth and fitness of the plant.

Table 4. Alleviation of heavy metals stress and enhancement of stress tolerance in plants after application of bioinoculants

Bioinoculants	Plants	PGP attributes	Effect on plant growth and soil condition	Reference
<i>Bacillus cereus</i> and <i>Alcaligenes faecalis</i>	<i>Sorghum vulgare</i>	IAA, GA, SA, and Proline accumulation	Enhanced plant growth and decreased heavy metals bioaccumulation in shoots and rhizosphere	El-Meihy et al. (2019)
<i>Bacillus megaterium</i>	<i>Pennisetum</i> sp.	Not presented	Enhanced plant biomass, chlorophyll, total nitrogen, and Cd accumulation	Kamal et al. (2021)
<i>Mucor</i> sp.	<i>Brassica campestris</i>	IAA, ACC deaminase and P-solubilization	Enhanced chlorophyll content, and overall plant growth. Reduced metal accumulation in the roots	Zahoor et al. (2017)
<i>Cellulosimicrobium funkei</i>	<i>Phaseolus vulgaris</i>	IAA, EPS, catalase production	Enhanced seed germination, total biomass, chlorophyll content, and carotenoid content	Karthik et al. (2016)
<i>Klebsiella</i> sp., <i>Enterobacter</i> sp.	<i>Zea mays</i>	IAA, EPS, catalase, phosphate solubilization	Enhanced shoot & root growth	Ahmad et al. (2015)
<i>Bacillus</i> sp.	<i>Solanum nigrum</i>	IAA, ACC deaminase, P-solubilization, siderophore production	Enhanced plant biomass	He et al. (2020)
<i>Enterobacter</i> sp.	<i>Pisum sativum</i>	IAA, siderophore production	Enhanced growth parameters, xanthophyll, carotenoid, and chlorophyll content	Naveed et al. (2020)
<i>Klebsiella pneumoniae</i>	<i>Oryza sativa</i>	IAA, ACC deaminase, P-solubilization, activity, N ₂ fixation	Enhanced seed germination, fresh weight, and total protein, chlorophyll, proline content	Mitra et al. (2018); Pramanik et al. (2017)
<i>Bacillus pumilus</i>	<i>Sedum plumbizincicola</i>	IAA, ACC deaminase, siderophore, and P-solubilization	Improved plant height and biomass, higher Cd uptake	Ma et al. (2015)
<i>Bacillus cereus</i> , <i>Providencia rettgeri</i> and <i>Myroides odoratimimus</i>	<i>Sorghum bicolor</i>	IAA, siderophores, P-solubilization, increased chlorophyll	Enhanced biomass (fresh and dry), and protein content	Bruno et al. (2020)
<i>Pseudomonas aeruginosa</i> , <i>Burkholderia gladioli</i>	<i>Lycopersicon esculentum</i>	Not presented	Enhanced fresh weight and decreased bioavailability of Cd.	Khanna et al. (2019)
<i>Glomus mosseae</i> , <i>Rhizobium trifolii</i> , <i>Brevibacillus brevis</i>	<i>Trifolium repens</i>	IAA production	Enhanced plant biomass, higher N, P content, and Ni amelioration	Vivas et al. (2006)
<i>Rahnella</i> sp.	<i>Brassica napus</i>	IAA, ACC deaminase siderophore, P solubilization	Enhanced phytoremediation of Cd, Pb, Zn in soil	He et al. (2013)
<i>Variovorax paradoxus</i> , <i>Rhodococcus</i> sp., <i>Flavobacterium</i> sp.	<i>Pisum sativum</i> , <i>Brassica juncea</i>	Not presented	Limited transfer of Cd from pea roots to shoots. Improved Cd mobilization in soil, Increase in root biomass and root nodulation frequency	Belimov et al. (2015)

3.1. Plant pathogens and their effects on plant growth

Infection by different pathogens, including bacteria, fungus, and viruses, not only lowers the yields but also depreciates the quality of produce. The effect and habitat range of different pathogens depend on climatic conditions. Various abiotic stresses negatively regulate the defence mechanisms of plants and enhance their vulnerability to infection (Suzuki et al., 2014). Photosynthesis is negatively affected by pathogen infection due to a decrease in stomatal conductance, and decreased leaf area index that alters the photosynthetic pigment function (Rho et al., 2022; Tseliou et al., 2021). *Peronospora plantaginis* and *Phytoplasma* infection reduce the total chlorophyll pigment of *Plantago ovata* and *Ziziphus jujuba* Mill (Chinese jujube) (Liu et al., 2016; Mandal et al., 2008). Pathogen infection also alters the plant's water relation and carbohydrate allocation pattern. Alteration in carbohydrate allocation in leaf tissue of *Manihot esculenta* (Cassava) plant infected by Cassava common mosaic virus (CsCMV) was observed (Zanini et al., 2021).

In pathogen-affected plants, ROS is mainly related to disease resistance responses but necrotrophs induce ROS production to their own advantage by the production of toxin and hydrolytic enzymes. Necrotrophs-generated ROS results in membrane damage and enables the entry of cellular content from cytoplasm which is used by pathogens for their own growth (Rossi et al., 2017).

Pathogens employ various strategies to alter the plant hormone homeostasis that enhances infection. Some pathogen have evolved strategies to suppress or manipulate the synthesis of salicylic acid (SA), jasmonic acid (JA), ethylene (ET) which significantly act in signalling and disease development. For example, *Ustilago maydis* infection produces chorismate mutase (CMU1), which induces the SA synthesis by converting chorismate to prephenate in the SA synthesis pathway. Another pathogen *Phytophthora sojae* and *Verticillium dahlia* secrete enzyme isochorismatase that can suppress SA accumulation by hydrolyzing isochorismate to 2,3-dihydro-2,3-dihydroxybenzoate (DDHB) and pyruvate thus enhancing the infection rate of the pathogen (Ma and Ma, 2016). Toxin coronatine (COR) produced by *P. syringae* enhances JA signaling by inducing degradation of JAZs (Jasmonate Zim-Domain protein), the higher concentration of JA induces reopening of the closed stomata and facilitate pathogen entry (Ma and Ma, 2016). In addition, pathogen infection also regulates nutrient uptake. A report from Li et al. (2018) on tomato plants indicated that the infection of *Fusarium oxysporum* reduces N and Cu uptake in comparison to non-infected plants.

3.1.1. Application of bioinoculants for controlling pathogens and stimulating plant growth

Bioinoculants inhibit pathogen infections by producing siderophore (Vandana et al., 2021), antibiotics, enzymes, and other chemicals; by inducing systematic resistance (ISR) (Nisrina et al., 2021; Oleńska et al., 2020; & Pieterse et al., 2014) that also upregulates endogenous defence hormones in plants (Ji et al., 2021) (Figure 2). Siderophore is a low molecular weight protein exuded by micro-organisms that sequester iron and makes it unavailable for the pathogens, hence restricting their growth (Nisrina et al., 2021). Siderophore producing *Enterobacter ludwigii* showing antagonistic activity against *Fusarium oxysporum* f. sp. *radicis-lycopersici* (FORL) enhanced root length and plant dry weight of tomato (*Solanum* sp.) plant (Bendaha and Belaouni, 2020). In another similar report from Ben Khedher et al. (2020) demonstrated that siderophore producing *Bacillus subtilis* decreased dry rot of the potato (*Solanum tuberosum*) plant caused by *Fusarium* sp. and enhanced plant growth.

In contrast, a range of low molecular weight secondary metabolites, such as antibiotics, are also produced by several microbial species (Figure 3). Many actinomycetes (8700), bacteria (2900), and fungi (4900) are known to produce antibiotics which can be exploited as biocontrol agents against several phytopathogens (Köhl et al., 2019). A recent molecular study conducted by QX Zhang et al. (2020) on antibiotic-producing *Pseudomonas protegens* FD6 confirmed that antibiotics are essential for antifungal activity. A similar study using *Streptomyces* spp. was reported against *Xanthomonas oryzae* (Hastuti et al., 2012) and *Fusarium oxysporum* f. sp. *ubense* (Zacky and Ting, 2013), responsible for bacterial leaf blight (BLB) in rice (*Oryza sativa*) and crown rot disease of banana (*Musa* sp.), respectively. A *Streptomyces* sp. strain A20 and *Bacillus licheniformis* strain HN-5 have also been reported for secretion of antibacterial compounds Streptotricins D, E, and F, (Suárez-Moreno et al., 2019), and non-ribosomal peptide antibiotic Bacitracin A (Jin et al., 2021), respectively.

Similarly, various hydrolytic enzymes, viz. chitinases, cellulases, proteases, and -glucanases, are produced by microbes dwelling in the rhizosphere that, directly and indirectly, support plant growth by suppressing phytopathogens. Plants, fungi, bacteria, protozoa, and arthropods all have cellulose, chitin, and glucan in their cell walls or exoskeletons (Poria et al., 2021). The glycosyl hydrolase family of enzymes includes cellulases, chitinases, and β -glucanases, which break down glycosidic linkages between carbohydrates and non-carbohydrate molecules. Chito oligosaccharides and β -1,4-N-acetylglucosamine are produced by ecto and endo chitinases as a result of chitin breakdown

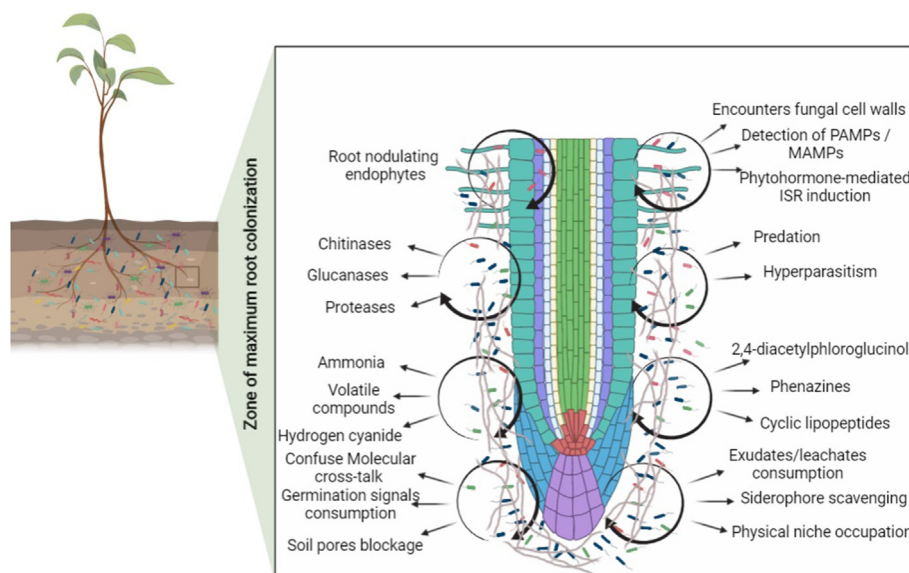


Figure 2. Biofertilizer microbes and plant (root) interaction in response to biotic stress.



Figure 3. Mechanism employed by various bioinoculants against different biotic stresses.

(Jadhav et al., 2017). Exochitinases act from the non-reducing ends of the chitin chain, whereas endochitinases act from anywhere along the chitin chain. Exo- β -1,3-glucanases, on the other hand, hydrolyze the glucan chain at random positions, while endo β -1,3-glucanases release glucose from the non-reducing end. Similarly, cellulases, interact with cellulose to cleave 1,4-D glucan bonds and release cello-oligosaccharide, cellobiose, and glucose as products.

Proteins are another important component of the cell wall of bacteria and fungi, where they perform adhesion, iron uptake, remodeling, and other functions in the organism. The activity of enzymes like protease that act on peptide bonds differs among filamentous fungi due to differences in cell wall compositions. Extracellular hydrolytic enzymes such as chitinases, β -1,3-glucanase, cellulases, and proteases have been recently reported in *Pseudomonas* sp. and *Bacillus* sp. (Akeed et al., 2020; Gómez-Lama Cabanás et al., 2018), *Priestia korensis* (Bashir et al., 2021), and *Serratia* sp. (Kshetri et al., 2019).

Besides antibiosis and siderophore production, the bioinoculants also defend the host through diverse defence strategies. SAR and ISR are two types of indirect ways of plant defence. SA and non-expression of pathogenesis-related genes (NPR) are major elements in SAR, whereas, ethylene and jasmonic acid signalling are essential elements in ISR (van Loon, 2007). Advantageous microbes can trigger ISR in plants by reinforcing plant cell walls, creating antimicrobial phytoalexins, and manufacture of pathogen related protein, in a similar way as pathogenic microbes. Several microbes have been known to induce ISR in plants, among these, nonpathogenic microbes belonging to the genus *Pseudomonas* spp., *Bacillus* spp., *Trichoderma* spp., *Serratia* spp. (pigmented) (Barman et al., 2020), *F. oxysporum* (Sajeena et al., 2020) are well reported (Figure 3) (Mandal and Ray, 2011; Newitt et al., 2019). Other indirect mechanisms include competition for root niches and nutrients, which have been supported by numerous studies (Di Francesco et al., 2017; Dwivedi and Johri, 2003; El-Maraghy et al., 2020; Rahman et al., 2021). Compatible host infection by most phytopathogen depends upon exogenous nutrient supply to achieve population efficiency to infect host tissue. Roots colonized by beneficial microbial communities or bio-inoculants take the nutrient for their growth making the rhizospheric niche nutrient deficient resulting in suppression of pathogens (Koskey et al., 2021). Some microorganisms compete for glucose and asparagine (Philippot et al., 2013). Mohamed and Caunter (1995) reported that

Pseudomonas fluorescens competes for glucose with *Bipolaris maydis*, the cause of corn leaf blight. Spadaro et al. (2010) and Spadaro and Droby (2016) showed that a fast root colonizing yeast and *Pichia guilliermondii* protected wound invasion by several phytopathogens in several fruits by consuming different mono and disaccharides along with some nitrogenous molecules in the carbohydrate-rich wound environment of fruits. The iron limitation is also a unique type of nutritional competition in which microbial siderophores attach to iron and render it unavailable to pathogens. Abo-Zaid et al. (2020) reported that *P. aeruginosa* F2 and *P. fluorescens* with optimized siderophore production decreased the *Fusarium oxysporum* causing damping-off in wheat. In a similar report, Yu et al. (2011) disclosed that the catechol type siderophore secreted by *B. subtilis* significantly demoted the incidence of *Fusarium* wilt disease in pepper and *Streptomyces* sp. with high siderophore production reported being efficient in the biocontrol of *Alternaria alternata* in tomatoes by Verma et al. (2011). Table 5 highlights various research outcomes on bioinoculants and their effects on crop tolerance to biotic stresses.

3.2. Herbivory and effects of different microbial inoculants to stimulate plant growth under herbivory

Herbivory is a type of biological relationship in which herbivore consumes autotrophs or their products. Plant progression and fecundity are largely distressed by aboveground herbivores, but belowground antagonists can also impact plant fitness and survival, either directly by damaging root tissue or indirectly by affecting relationships with other microbes (Nunes and Kotanen, 2018). Around 20–40% of agricultural yield is lost owing to various types of herbivories, whereas 15% of yield is worldwide lost to herbivory by insects (van der Meijden, 2015).

Several microbes that are used as biofertilizers or biocontrol agents induce defence against above and below-ground herbivores either directly by acting as entomopathogens or indirectly via ISR (Disi et al., 2019). Lipopolysaccharides, pyocyanin, 2,4-diacetylphloroglucinol, lipopeptides, volatiles, and iron-regulated substances are the key determinants of PGPR-mediated ISR (Meena et al., 2020). Upon interaction of host plant and beneficial microbes, defence hormonal signal pathways like JA, ET, SA are upregulated, which enhances the synthesis of defence-related chemical compounds, such as secondary metabolites (alkaloids, phenols, nonvolatile terpenes), enzymes, and volatile organic

Table 5. Effects of different microbes as bioinoculants in the alleviation of biotic stress and enhancement of stress tolerance in plants.

Bioinoculants	Pathogen/Insect	Host	Effect on host plant	Mode of action	Reference
<i>Azospirillum lipoferum</i>	<i>Alternaria solani</i>	<i>Solanum tuberosum</i>	Enhanced plant growth, reduced pathogen severity	Enhanced defence-related enzyme peroxidase, polyphenol oxidase, phenylalanine ammonia lyase, and salicylic acid level	Mehmood et al. (2020)
<i>Trichoderma rossicum</i> and <i>T. harzianum</i>	<i>Alternaria alternata</i>	<i>Malus sieversii</i>	Enhanced lateral root growth, and, reduced numbers of disease spots	Enhanced cell membrane permeability and jasmonic acid content	Ji et al. (2021)
<i>Bacillus subtilis</i>	<i>Fusarium</i> spp.	<i>Solanum tuberosum</i>	Enhanced fresh weights of plant, and reduced lesion diameter and the rot penetration	Enhanced Siderophore, hydrolytic enzymes and some other antimicrobial compound production	Ben Khedher et al. (2020)
<i>Streptomyces violaceusniger</i>	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	<i>Musa</i> sp.	Enhanced plant growth and inhibit the infecting agent significantly	Enhanced Production of 5-hydroxymethyl-2-furancarboxaldehyde and hydrolytic enzyme and other antimicrobial compound	Jing et al. (2020)
<i>Bacillus thuringiensis</i> and <i>Bacillus velezensis</i>	<i>M. incognita</i>	<i>Solanum lycopersicum</i>	Enhanced shoot growth root, fresh weight, and show intense toxic effect against hatchling and juvenile	Enhanced production of hydrolytic enzymes	Choi et al. (2020)
<i>Enterobacter ludwigii</i>	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>	<i>Solanum lycopersicum</i>	Enhanced root length, plant dry weight, and antagonistic activity	Enhanced siderophore production and IAA phosphates solubilization	Bendaha and Belaoumi (2020)
<i>Bacillus</i> spp.	<i>Sclerotium rolfsii</i> <i>Fusarium oxysporum</i> , <i>Colletotrichum capsici</i> , and <i>Pythium aphanidermatum</i> ,	<i>Solanum lycopersicum</i>	Enhance growth parameter and yield of plant and reduced disease incidence of damping-off, root rot, leaf spot, and wilt	Enhanced siderophore, IAA phosphates solubilization	Amareesan et al. (2019)
<i>Brettanomyces naardensis</i>	<i>Macrophomina phaseolina</i>	<i>Helianthus</i>	Enhanced plant height, and weight and, leaf number, and reduction of the disease incidence of root rot and charcoal rot	Induction of the immune system via decreasing malondialdehyde content (MDA)	Nafady et al. (2019)
<i>Streptomyces violaceoruber</i>	<i>Colletotrichum capsici</i>	<i>Capsicum</i> sp.	Improved germination, higher chlorophyll content, plant growth, and reduced disease incidence (anthracnose)	Not presented	Thilagam and Hemalatha (2019)
<i>Metarhizium brunneum</i>	<i>Agriotes lineatus</i> Wireworms	<i>Zea mays</i>	Enhanced plant growth and reduced <i>Agriotes</i> herbivory	Not presented	Razinger et al. (2020)
<i>M. robertsii</i>	Black cutworm, <i>Agrotis ipsilon</i> (Hufnagel)	<i>Zea mays</i>	Enhanced plant growth	Increase defence related gene expression (lipoxygenase 1, 12-oxo-phytodienoate reductase 7, endochitinase A) and decrease pathogenesis-related protein gene	Ahmad et al. (2020)
<i>Bacillus pumilus</i> , and <i>Bacillus sphaericus</i>	Tawny mole crickets	<i>Cynodon dactylon</i>	Enhanced growth and tolerance of Bermuda grass to damage from tawny mole crickets	Not presented	Coy et al. (2020)
<i>Piriformospora indica</i>	<i>Lissorhoptrus oryzophilus</i>	<i>Oryza sativa</i>	Induce plant growth and tolerance to root herbivory	Reduced herbivore-mediated JA synthesis and enhanced GA	Cosme et al. (2016)
<i>Bacillus amyloliquefaciens</i>	<i>Spodoptera exigua</i> , <i>Plutella xylostella</i>	<i>Arabidopsis</i> sp., <i>Eruca sativa</i>	Enhanced plant growth, seed germination and plant biomass enhanced significantly	Enhanced upregulation of sulfur assimilation and glucosinolate biosynthetic genes	Cristina dos Santos et al. (2021)
<i>Azospirillum lipoferum</i>	<i>Alternaria solani</i>	<i>Solanum tuberosum</i>	Enhanced plant growth, reduced pathogen severity	Enhanced defence-related enzyme peroxidase, polyphenol oxidase, phenylalanine ammonia lyase, and salicylic acid level	Mehmood et al. (2020)

compounds (Figure 3) (Harun-Or-Rashid and Chung, 2017). For example, *Arabidopsis* plants treated with rhizobacterium *Pseudomonas simiae* WCS417r trigger JA/ET upregulation, which directs the enhanced endogenous synthesis of phytoalexins like camalexin and glucosinolates in plants (Pangesti et al., 2016). Some microbes showed entomopathogenicity, for example, *Bacillus thuringiensis* (Bt), *Photorhabdus* sp., and *Xenorhabdus* sp. (Disi et al., 2019). Microbes also induce structural modification and antibiosis in host plants against herbivores. Inoculation of *Metarhizium brunneum* and *Metarhizium robertsii* enhances stand density and yield of a *Zea mays* (maize) plant by enhancing the mortality rate of *Agriotes lineatus* at the larval stage (Razinger et al., 2020) and by suppressing the growth rate of Black cutworm (*Agrotis ipsilon*), respectively (Ahmad et al., 2020). Another research conducted by Cosme et al. (2016) showed that inoculation of the endophytic fungus *Piriformospora indica* enhances tolerance of *Oryza sativa* (rice) plants against below-ground herbivory by *Lissorhoptrus oryzophilus*. Some strains of PGPB are also significant in herbivory resistance like *Bacillus pumilus* and *Bacillus sphaericus* that enhance growth and tolerance of *Cynodon dactylon* (Bermuda grass) against tawny mole crickets (Coy et al., 2020) and

another strain of *B. amyloliquefaciens* show good protection against common herbivores (Table 5).

4. Conclusion and future prospects

- Several biological and technological constraints impede the adoption and widespread use of bioinoculants. Bioinoculants being a low value commodity, is less rewarding venture for entrepreneurs with only few major quality producers in most of the countries. Poor awareness about bioinoculants among farmers and short self-life of bioinoculants makes the adoption of bioinoculants a challenging task.
- Climate change is projected to exaggerate biotic and abiotic stresses that potentially can threaten the sustainable crop production. Adoption of organic agricultural practices like integrated pest management, use of bioinoculants and botanicals can help in enduring climate change and will reducing dependence on chemicals. The demand for bioinoculants is anticipated to be significant in the future, however the farmer's perception about bioinoculants is not very encouraging. Extension agencies need to play a principal role in

popularizing the bioinoculants by undertaking more field demonstration and training of farmers on application and in-farm production of selected inoculants. In addition, researchers should also focus to develop bioinoculant application methods that are similar to chemical fertilizer so that even unskilled farmers may employ them.

- The bioinoculants not only increase crop production by strengthening the plant's defence system and protecting it from drought, salinity, and other biotic stresses but also improve soil health. Recently, the use of a consortium of microorganisms in crop production is being advocated as a single bioinoculant may not be sufficient to provide nutrients and protect plants from multiple stresses. Diverse soils and different agro-climatic zones restrict the development of an effective formulation for all regions; therefore, strategies must be focused on the selection of efficient native strains for better results. However, the compatibility and competitive saprophytic ability testing of the consortium is a challenging task. The bioinoculants must be tested at multiple locations before commercialization to avoid any failure of bioinoculants at field level.

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