



REVIEW ARTICLE

Microbe mediated drought stress mitigation: A review

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Abstract

Drought is one of the most critical abiotic stresses limiting crop growth, productivity and yield by adversely affecting essential physiological and biochemical processes, including seed germination, photosynthesis, nutrient uptake, osmotic regulation and cellular homeostasis. The increasing frequency and severity of water-deficit conditions due to climate change necessitates the development of sustainable strategies to enhance plant drought tolerance. Beneficial microorganisms have emerged as key contributors to improving plant resilience under drought stress by facilitating water and nutrient acquisition, reinforcing antioxidant defense systems and regulating stress-responsive pathways. Plant growth-promoting rhizobacteria, endophytic bacteria and fungi, including arbuscular mycorrhizal fungi (AMF), play a vital role in mitigating drought through multiple mechanisms such as osmolyte accumulation, activation of antioxidant enzymes, modulation of phytohormone levels, degradation of stress-induced ethylene via 1-aminocyclopropane-1-carboxylic acid deaminase (ACCd), exopolysaccharide production, emission of volatile organic compounds (VOCs) and alteration of root system architecture. Application of microbial inoculants has consistently demonstrated improvements in plant growth, water-use efficiency and yield stability under water-limited conditions. Integrating beneficial microbes into crop management practices offers a sustainable, eco-friendly and cost-effective strategy for climate-resilient agriculture, reducing dependency on chemical inputs while ensuring productivity and food security under increasingly arid and unpredictable environmental conditions.

Keywords: 1-aminocyclopropane-1-carboxylic acid deaminase; antioxidant defense; biopriming; exopolysaccharides; mycorrhiza; phytohormones

Introduction

Climate change represents a major challenge to the long-term sustainability of agriculture worldwide. Rising temperatures associated with global warming are expected to increase evapotranspiration rates of crop plants in many regions, thereby escalating irrigation demands. Coupled with declining precipitation, these changes present significant challenges to food security in the future. The global report on food crises (2024) highlights that more than 287 million people across the world experienced severe acute food insecurity during 2024 (1). Abiotic stresses account for approximately 50 % of agricultural productivity losses, while biotic stresses contribute about 30 % (2). To prevent escalating food crises, it is imperative to address both biotic and abiotic stresses that constrain crop yields. Key abiotic stresses include drought, waterlogging, salinity, extreme temperatures, soil acidity or alkalinity, heavy metal contamination and nutrient deficiencies (3). Among these, drought is the most devastating, causing substantial global yield reductions. Drought alone can reduce crop yields by up to 48 %, exceeding the combined effects of other abiotic stresses (4).

Drought stress is a major constraint on crop productivity, adversely impacting plant growth from seed germination through subsequent developmental stages to final yield. Drought stress disrupts early plant establishment by limiting soil moisture, thereby

severely impairing germination and subsequent seedling development (5). Prolonged drought stress disrupts fundamental cellular processes, including cell division and elongation, thereby constraining vegetative growth and overall plant development (6). The decline in vegetative vigour is further compounded by reduction in photosynthetic capacity, attributable to restricted leaf expansion, damage to the photosynthetic apparatus and premature leaf senescence (7). In parallel, drought stress impairs nutrient acquisition by decreasing nutrient uptake efficiency of the roots and limiting nutrient transport through the transpiration stream (8). Compounding these physiological disruptions, drought also triggers oxidative stress through the overproduction of reactive oxygen species (ROS), such as superoxide radicals, hydrogen peroxide (H₂O₂) and singlet oxygen, which inflict damage on cellular macromolecules, including lipids, proteins and nucleic acids (9). The cumulative impact of these physiological and biochemical perturbations has had substantial implications for global agriculture. Over the past 35 years, drought has led to considerable yield losses in major crops, with reductions of approximately 10 % in rice, 21 % in wheat, 40 % in maize and up to 60 % in chickpea (10). Projections for the future are equally concerning, with estimates suggesting that by 2052, nearly 50 % of cultivable land could be severely constrained in its capacity to support optimal plant growth due to water limitations (11).

Multiple approaches are employed to mitigate abiotic stresses and enhance crop productivity, such as breeding climate-resilient varieties via conventional and advanced breeding, application of plant growth regulators and osmo-protectants, optimised nutrient and water management and adjusted sowing schedules. Among these, the deployment of beneficial microbial strains represents a feasible, reliable, eco-friendly and sustainable approach to alleviating abiotic stresses in plants (12).

Microbes involved in drought mitigation

Microorganisms contribute to drought tolerance in plants by facilitating efficient absorption of water and nutrients even under stressful conditions. Predominantly, these include bacteria and fungi that help to maintain plant water balance, extending survival during prolonged dry periods. This makes them invaluable for optimising crop performance in water-scarce environments.

Bacteria

Bacteria contribute significantly to plant drought tolerance through mechanisms that bolster resilience and survival. These plant growth-promoting bacteria encompass endophytic bacteria and rhizobacteria. The rhizosphere, a dynamic ecosystem surrounding plant roots harbours diverse microorganisms, including bacteria, actinobacteria, archaea, fungi, algae and protozoa. They engage in mutualistic, commensal, neutral, exploitative, or competitive interactions with plants (13). Certain rhizosphere bacteria and fungi can invade plant tissues to become endophytes. Endophytes, comprising fungal and bacterial species, reside asymptotically within plant tissues and promote growth under stresses like drought, salinity, or nutrient scarcity (14).

A group of microbes known as plant growth promoting rhizobacteria (PGPR) colonise the rhizosphere and contribute to the enhancement of plant growth (15). The rhizosphere represents a nutrient-enriched soil zone where microbial population can reach densities of upto 10^{12} cells per gram of soil, with diversity levels of magnitude higher than those observed in the bulk soil (16). Plant growth promoting rhizobacteria enhances plant development, improves tolerance to drought stress and plays an important role in advancing sustainable agriculture (Table 1 and 2).

Fungi

Beneficial fungi assist plants in coping with drought stress by inhabiting plant tissues as endophytes or forming mutualistic associations with roots (Table 3 and 4). Endophytic fungi colonise host tissues intercellularly or intracellularly during part or all of their life cycle without inducing visible disease symptoms. Fungal endophytes have proven to be a safe and economical means of achieving sustainable farming because of their capacity to generate bioactive chemicals, growth hormones and increased nutrient uptake, all of which aid in the promotion of host plants. To understand the role of endophytic fungi in drought mitigation, it is essential to study root-associated fungi, as roots are the primary organs of water-absorption by plants. Root endophytic fungi, such as dark septate endophytic fungi, *Serendipita* (= *Piriformospora*) *indica* is one such example. In contrast, mycorrhizal fungi, particularly arbuscular mycorrhizal fungi (AMF), establish associations with root cortical cells where arbuscules are formed for metabolite exchange (45, 46). Their extraradical hyphae further facilitate nutrient and water absorption while improving soil aggregation and structure (47). One characteristic that distinguishes

Table 1. List of endophytic bacteria for drought mitigation with its mechanism of action

Endophytic bacteria	Crop	Mechanism of action	References
<i>Bacillus cereus</i> and <i>Enterobacter mori</i>	Maize	Accumulation of osmolytes and secondary metabolites	(17)
<i>B. safensis</i> COBR7	Chickpea	Production of superoxide dismutase (SOD) and 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity	(18)
<i>B. velezensis</i> S141	Soyabean	Improved root growth	(19)
<i>B. pumilus</i> SH-9	Rice	Production of SOD, catalase (CAT) and ascorbate peroxidase (APX)	(20)
<i>B. pumilus</i>	Ural licorice	Modification of root architecture and accumulation of soluble sugar	(21)
<i>B. amyloliquefaciens</i> LAS10	Little millet	ACCD activity and production of exopolysaccharides (EPS)	(22)
<i>Gluconacetobacter diazotrophicus</i> Pal5	Rice	Antioxidant enzyme activity	(23)
<i>B. subtilis</i>	Pepper	Synthesis of volatile organic compounds (VOCs)	(24)

Table 2. List of plant growth promoting rhizobacteria for drought mitigation with its mechanism of action

Plant growth promoting rhizobacteria	Crop	Mechanism of action	References
<i>Acinetobacter calcoaceticus</i> AC06 and <i>B. amyloliquefaciens</i> BA01	Groundnut	Accumulation of osmolytes and antioxidants	(25)
<i>B. amyloliquefaciens</i> MMRO4	Pearl millet	ACC deaminase activity	(26)
<i>B. licheniformis</i> FMCH001	Maize	Upregulation of antioxidative enzyme	(27)
<i>Pseudomonas</i> sp. N66	Sorghum	Antioxidant activity and root architecture modification	(28)
<i>P. chinense</i> , <i>B. cereus</i> and <i>P. fluorescens</i>	Wheat	Enhanced production of proline and antioxidant enzyme	(29)
<i>Enterobacter bugandensis</i> WRS7	Wheat	Increases chlorophyll content	(30)
<i>B. paranthracis</i> DT-97 and DT-85	Wheat	Production of EPS, indole-3-acetic acid (IAA), and ACC deaminase	(31)
<i>B. subtilis</i> Rhizo SF 48	Tomato	ACCD activity	(32)
<i>Ochrobactrum anthropi</i> , <i>P. palleroniana</i> and <i>P. fluorescens</i>	Wheat	ACCD activity	(33)
<i>B. subtilis</i> and <i>Azospirillum brasilense</i>	Wheat	Production of EPS	(34)
<i>P. pseudoalcaligenes</i>	Maize	Emission of microbial VOCs	(35)

Table 3. List of fungal endophytes for drought mitigation with its mechanism of action

Endophytic fungi	Crop	Mechanism of action	References
<i>Piriformospora indica</i>	Rice	Accumulation of proline and modification of root architecture	(36)
<i>P. indica</i>	Rice	Accumulation of proline	(37)
<i>Zygorrhiza eriostrata</i>	Wheat	Accumulation of proline	(38)
<i>P. indica</i>	Tomato	Modification of root architecture and antioxidant activity	(39)
<i>Acrocalymma vagum</i>	<i>Ormosia hosiei</i>	Alterations in photosynthetic characteristics	(40)

Table 4. List of arbuscular mycorrhizal fungi for drought mitigation with its mechanism of action

Arbuscular mycorrhizal fungi	Crop	Mechanism of action	References
<i>Glomus versiforme</i>	Maize	Accumulation of solute and maintaining relative water content	(41)
<i>Rhizophagus intraradices</i> and <i>R. fasciculatum</i>	Tomato and bellpepper	Antioxidant activity	(42)
<i>G. intraradices</i>	Barley	Improve phosphatase activity and proline accumulation	(43)
<i>Glomus</i> sp. and <i>Paraglomus</i> sp.	Watermelon	Improved water use efficiency	(44)

mycorrhizal fungi from endophytic fungi is that mycorrhizal fungi are obligate biotrophs and cannot survive without their plant hosts.

Mechanism employed by microbes for drought stress mitigation

Accumulation of solutes

Microbial inoculants have emerged as promising allies in helping plants withstand drought by enhancing the accumulation of osmolytes, compounds that protect cells under stress. For instance, *P. indica* was found to boost proline levels in watermelon grown under water-limited conditions, thereby improving the plant stress adaptability (37). Similarly, PGPR like *A. calcoaceticus* and *B. amyloliquefaciens* played a crucial role in enhancing drought tolerance in groundnut by stimulating the production of proline, trehalose, glycine betaine and salicylic acid (25). In the case of okra, seeds primed with *B. subtilis* showed increased accumulation of proline and soluble sugars, which helped the plants recover more effectively from drought stress (48).

Plant tolerance to drought is closely tied to the accumulation of certain organic and inorganic secondary metabolites within their cells, particularly in the cytosol. These compounds play a critical role in helping plants adjust osmotically under water-deficient conditions. During drought, they get accumulated in the cytoplasm, effectively lowering water potential of the cells, maintaining the turgor pressure, allowing the plant to continue absorbing water while preserving vital metabolic functions (49, 50).

Interestingly, beneficial microbes further amplify this protective mechanism. They not only produce osmolytes themselves but also secrete them along with other root exudates into the rhizosphere. Microbially derived osmolytes, together with plant-produced molecules like proline, betaine, trehalose and various soluble sugars, function as effective osmoprotectants. Together, they safeguard plant cells from dehydration-induced damage and help sustain cellular integrity during periods of water deficit (51). In rice plants colonised by *P. indica* and subjected to intense drought stress, leaf proline concentrations increased by 18 % at the panicle initiation stage and by 21 % at flowering, relative to non-inoculated controls. *P. indica* colonisation improved relative leaf water content and stabilised cell membranes, contributing to better stress tolerance (52).

Among these, proline stands out as a multifunctional molecule. This proteinogenic amino acid is not only fundamental to primary metabolism but also possesses structural rigidity that makes it especially effective during stress. Its accumulation in plants during drought plays a multifaceted role as it aids in osmotic

balance, scavenges harmful free radicals, reduces lipid peroxidation, stabilises cellular membranes and modulates reactive oxygen species (ROS), all of which contributes to enhanced drought resilience (53, 54).

The benefits of microbial assistance extended to cereals as well. *G. versiforme*, an AMF, significantly increased the levels of compatible solutes in maize, enabling better drought resilience even under severe stress (41). Likewise, pink-pigmented facultative methylotrophs (PPFMs) contributed to enhanced drought tolerance in rice by promoting proline accumulation (55). Taken together, these findings signify the role of beneficial microbes as eco-friendly and sustainable agents in mitigating drought stress through osmolyte-mediated pathways.

However, current studies seldom distinguish between osmolytes produced by plants and those exuded from microbes and then taken up by roots. Stable isotope labeling or tracing of metabolites could explain if observed increases are due to microbial production, plant biosynthesis, or a combination of both. Also, most reports are based on pot or greenhouse studies with controlled drought regimes. Only a few field-scale trials under diverse soil types, climates and cropping systems have been conducted so far. Understanding how such inoculants work under fluctuating moisture conditions and in concert with native microbiomes will be important for the development of reliable microbial formulations.

Antioxidant activities and accumulation of reactive oxygen species

Under drought-induced osmotic stress, plants experience excessive accumulation of ROS, such as H₂O₂, singlet oxygen and superoxide radicals, which can cause oxidative damage to lipids, proteins and nucleic acids, ultimately disrupting stability of internal cellular environment (56). Lipid peroxidation, a key consequence of ROS attack on polyunsaturated fatty acids in membranes, compromises membrane integrity and function. Malondialdehyde (MDA), produced during lipid peroxidation, is widely utilised as a biochemical marker to quantify oxidative stress and membrane damage during drought stress (57).

In response to oxidative stress from ROS, plants trigger a complex antioxidant defense network that encompasses enzymatic as well as non-enzymatic elements. Key enzymatic antioxidants such as SOD, CAT, APX and glutathione reductase work in tandem with non-enzymatic molecules like glutathione, cysteine and abscisic acid (AA) to neutralise ROS and maintain cellular homeostasis (12). The enhanced activity of these enzymes is strongly linked to improved drought tolerance in plants. Recent studies have shown that microbial inoculants can further amplify this antioxidant

defense. Microbial species including strains like *A. calcoaceticus* and *B. amyloliquefaciens*, have been demonstrated to significantly boost the activities of CAT, APX and SOD in groundnut under both mild and severe drought stress, thereby minimising ROS accumulation and improving stress resilience (25). *Bacillus pumilus* strain SH-9, a newly identified member of the Bacillaceae family, exhibits strong antioxidant activity (CAT, SOD, APX), demonstrating its potential utility in seed biopriming for augmenting drought tolerance in *Oryza sativa* (20).

Similarly, microbial consortia involving *Azotobacter*, *Enterobacter*, *Lactococcus*, *P. indica* and AMF were found to increase antioxidant enzyme activity in wheat grown under limited moisture conditions (58). Inoculated wheat plants exhibited elevated levels of SOD, CAT and APX, suggesting an enhanced ability to manage oxidative stress. A similar pattern appeared in tomato plants treated with *P. indica*, which exhibited notably elevated antioxidant enzyme levels during drought stress relative to untreated controls (39). In rice, drought tolerance was likewise reported to be improved through the application of PGPR strains such as *P. fluorescens*, *B. cereus* and *Arthrobacter* spp., which not only enhanced antioxidant enzyme activity but also reduced oxidative stress indicators like H_2O_2 and MDA (59).

The overall results of previous studies indicate that microbial inoculation significantly enhances the antioxidant defense system of the plant under drought stress by increasing the activities of SOD, CAT and APX, which reduces ROS accumulation and lipid peroxidation. However, most of them lack specific information on which microbial metabolites or signalling pathways are involved in the activation of plant antioxidant machinery. Future studies need to include a combined approach of molecular and biochemical analyses to unravel such mechanisms.

Phytohormone modulation

Phytohormones are core regulators of plant growth and stress adaptation, particularly under drought conditions. Key hormones such as IAA, gibberellins (GA), AA, cytokinins and ethylene play essential roles in regulating root architecture, stomatal behaviour and overall plant development during water deficit (60). Indole-3-acetic acid, the primary auxin, is vital for cell elongation and root system development. Drought stress often suppresses endogenous auxin synthesis; however, IAA-producing rhizobacteria can compensate for this deficiency by enhancing lateral root and root hair development, thereby improving water and nutrient uptake (61, 62). Gibberellins support stem elongation and leaf expansion, helping maintain vegetative growth during moderate stress. Absciscic acid, on the other hand, promotes stomatal closure, thus minimising water transpiration loss and improving water-use efficiency (63).

Several investigations have shown that microbial inoculants can modulate phytohormone levels in plants under drought conditions. For instance, *E. bugandensis* WRS7 enhanced wheat performance under drought by boosting growth traits and chlorophyll content, largely due to its IAA and GA production (30). Similarly, *B. paranthracis* DT-97 and *B. paramycoides* DT-85 notably improved shoot and root development, increased chlorophyll content and expanded leaf area in wheat under water-limited conditions. Among these, DT-97 showed superior performance, suggesting its potential as a promising bioinoculant for drought-prone agroecosystems (31). Microbial production of phytohormones rebalances stress-altered signalling networks, promoting adaptive

growth, efficient stomatal regulation and improved water-use efficiency under drought.

Activity of 1-aminocyclopropane-1-carboxylate deaminase

Ethylene production in plants is triggered by a wide range of abiotic and biotic stresses, including extreme temperatures, salinity, drought, flooding, heavy metal exposure, chemical treatments, nematode infestation and pathogen attacks (64). Under such conditions, plants produce 'stress ethylene' which accelerates senescence by activating ethylene-responsive genes (65). The biosynthesis of ethylene follows a straightforward metabolic pathway in which methionine is first converted into S-adenosyl methionine, which is then transformed into ACC by the enzyme ACC synthase (ACS). Finally, ACC oxidase converts ACC, the immediate precursor into ethylene (66). Excessive ethylene accumulation under stress conditions can inhibit plant growth and reduce productivity, highlighting the importance of mitigating ethylene-induced damage to enhance crop performance.

1-aminocyclopropane-1-carboxylic acid deaminase producing rhizobacteria utilise root-exuded tryptophan and other small molecules to synthesise IAA, which, together with endogenous plant IAA, influences plant developmental processes and promotes ACS gene expression for ACC synthesis (67). The ACC thus produced induces bacterial ACCD activity, which hydrolyses ACC into ammonia and α -ketobutyrate, thereby lowering ethylene production and enhancing water and nutrient uptake through modifications in root architecture (68).

The role of ACCD-producing microbes in enhancing drought tolerance has been demonstrated across various crops. In tomato, *B. subtilis* Rhizo SF 48 has been shown to reduce oxidative stress and downregulate ethylene-responsive gene expression under severe drought, thereby improving water retention and physiological performance (32). In wheat, a microbial consortium consisting of *O. anthropi*, *P. palleroniana* and *P. fluorescens* improved growth and foliar nutrient concentrations under water-limited conditions (33). Similarly, *Burkholderia phytofirmans* strain PsJN enhanced wheat performance under drought by limiting ethylene biosynthesis through ACCD activity, with the most notable effects observed during the tillering stage (69).

The reviewed literature supports the conclusion that ACCD-producing microbes mitigate drought stress by modulating ethylene biosynthesis, preventing its excessive accumulation and delaying senescence. This regulation maintains hormonal equilibrium, sustains root and shoot development and optimises water and nutrient uptake, thereby enhancing plant resilience and productivity under water-deficit conditions. Future research should focus on identifying plant genes responsive to microbial ACCD action, quantifying threshold levels of ACC reduction required for optimal stress mitigation and evaluating the long-term stability of ACCD-mediated effects under variable field conditions.

Production of exopolysaccharides

Exopolysaccharides (EPS) are complex, high-molecular-weight biopolymers consisting of recurring sugar residues like glucose, galactose and rhamnose, often accompanied by small quantities of proteins and uronic acids (70). These compounds are secreted by soil dwelling microbes in the form of slime or capsules and interact with soil particles through hydrogen bonding, Van der Waals forces and anion exchange, contributing to the formation of a protective matrix around the soil (34). This matrix contributes to better soil

architecture through enhanced aggregation and macroporosity, thereby promoting soil biological activity and increasing water-holding capacity. In addition to modifying the soil environment, EPS plays a vital role in promoting root colonisation, nodule formation, biofilm development and plant defense responses, thereby enhancing the ability of plants to withstand stress (71).

Priming wheat seeds with drought-tolerant EPS-producing bacterial strains such as *B. subtilis* and *A. brasilense*, either individually or in combination, has been shown to significantly enhance drought resilience in wheat cultivars (34). Plants inoculated with this microbial consortium demonstrated improved shoot and root growth under both well-watered and drought-stressed conditions. These positive effects are largely linked to increased EPS synthesis, which aids in soil moisture retention, facilitates microbial colonisation and supports plant adaptive mechanisms during water-deficit stress.

The literature provides evidence that ACCD-producing microbes alleviate drought stress by adjusting ethylene biosynthesis and preventing its excessive accumulation, delaying senescence. This regulation maintains the hormonal balance, optimises root and shoot development and enhances water and nutrient uptake, which results in improved resiliency and productivity of plants under water-deficit conditions. Future studies are needed to identify plant genes responsive to microbial ACCD action, quantify threshold levels of ACC reduction required for optimal stress mitigation and test the long-term stability of ACCD-mediated effects under variable field conditions.

Emission of microbial volatile organic compounds

Volatile organic compounds of microbial origin are small lipophilic molecules with a molecular weight typically below 300 g mol^{-1} and they can be emitted by both plants and microbes during growth or under stress conditions (72). In plants, stress-induced VOCs, including isoprenoids, function as protective agents by neutralising ROS and maintaining membrane integrity, thereby enhancing stress

resistance (73).

Volatile compounds released by *P. pseudoalcaligenes* are reported to induce systemic tolerance in maize exposed to drought stress (35). Maize plants exposed to microbial VOCs exhibited lower electrolyte leakage and MDA accumulation compared to untreated controls under drought conditions. In addition, treated plants showed increased levels of photosynthetic pigments, proline and phytohormones, as well as enhanced activity of antioxidant enzymes in both roots and shoots. These results demonstrate the capacity of microbial VOCs to mitigate drought-induced oxidative damage and support key physiological and biochemical processes that underpin plant stress tolerance. Microbial VOCs play a vital role in conferring drought tolerance by activating systemic defense responses, enhancing antioxidant activity and maintaining photosynthetic efficiency. By reducing oxidative damage and preserving membrane integrity, these volatiles help plants sustain growth and metabolic functions under water-limited conditions.

Modification in plant architecture

Root system architecture is fundamental to plant adaptation under drought, as it governs water and nutrient acquisition, provides structural stability and mediates interactions with beneficial soil microorganisms. Colonisation of the rhizosphere by microbes can trigger morphological as well as physiological changes in roots, which in turn enhance plant growth and improve tolerance to stress. In maize, the application of a tri-inoculant consortium comprising *S. indica*, *R. intraradices* and *Azotobacter chroococcum* (SRA) has been shown to mitigate the adverse impacts of drought stress (74). Although drought conditions caused an overall reduction in shoot and root growth, the decline was significantly less pronounced in SRA-treated plants. These inoculated plants exhibited longer shoots and roots, along with higher fresh and dry biomass, suggesting enhanced resource acquisition and greater resilience under water-deficit conditions (Fig. 1).

In rice, colonisation by *P. indica* under varying irrigation

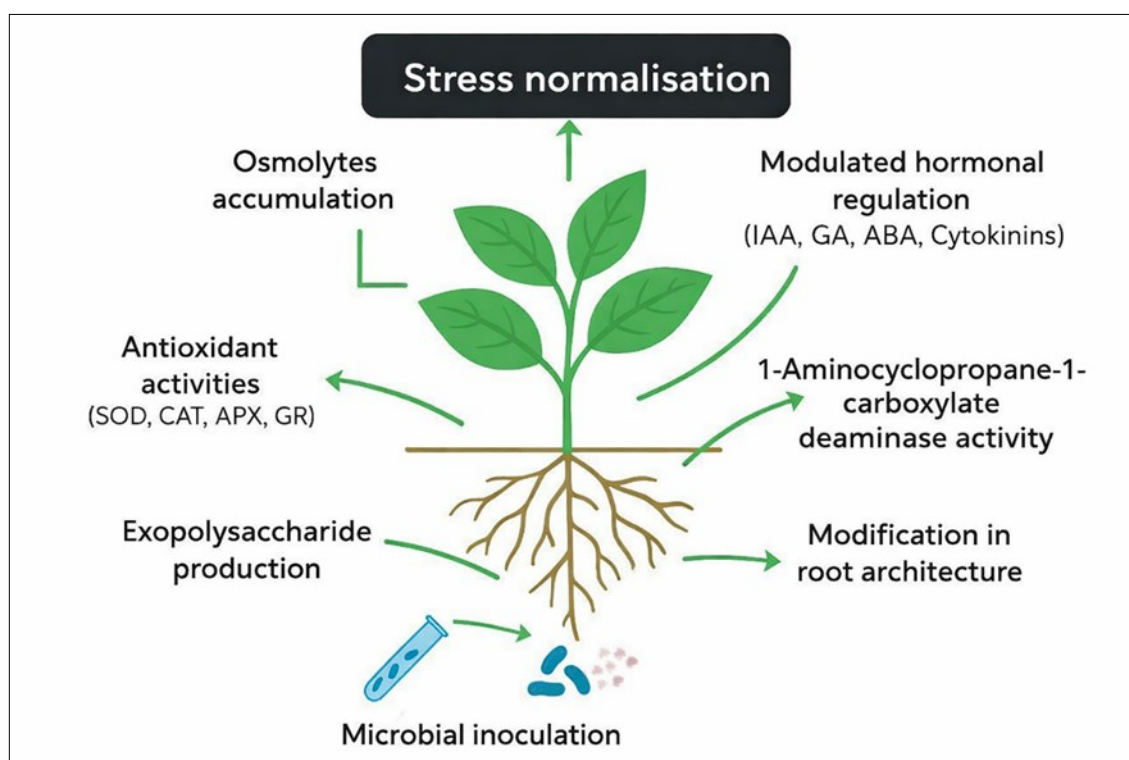


Fig. 1. Mechanism employed by microbes for drought stress mitigation.

intervals and depths significantly influenced root development at all growth stages (75). Greater root volume was recorded in colonised seedlings, particularly under conditions of moderate irrigation frequency and depth. This expanded root system allowed for more effective water absorption, helping to maintain leaf water content and plant hydration under drought conditions. A similar effect was observed in black pepper, where *P. indica*-colonised plants consistently produced a greater number of leaves and exhibited larger leaf area compared to uninoculated control (76). Enhanced vegetative growth in colonised plants reflected the role of fungus in promoting overall plant vigour, contributing to better drought adaptation. *Bacillus velezensis* S141 stimulates soybean root development during water scarcity by enhancing root dry matter accumulation, thereby contributing to improved drought tolerance (19).

While there is a need to consider evidence from several investigations, it can be inferred that beneficial microbes trigger adaptive changes in root architecture for improved water uptake, sustaining plant vigour during drought. However, molecular dialogue between microbial colonisation and root developmental regulators, including but not limited to auxin transporters, aquaporins and transcription factors responsible for lateral root formation, remains poorly understood. Furthermore, the persistence of such root modifications under fluctuating field moisture regimes and interaction with native rhizosphere microbiota have not been substantially validated. Future studies must therefore identify microbial signals modulating root growth genes, quantify their long-term effects on water uptake efficiency and assess multi-strain inoculants under field conditions for consistency and scalability in drought-prone cropping systems.

Practical application

Pink pigmented facultative methylotroph liquid formulations are recommended for all field crops (through foliar application at

200 mL/acre, diluted in 200 L of water) to alleviate drought stress. Likewise, AMF inoculants are commercially available and used as biofertilisers to enhance plant resilience under water deficit. Biopriming, which involves soaking seeds in microbial suspensions, effectively improves germination, seedling vigour and stress tolerance. In addition, microbial consortia composed of compatible strains provide synergistic effects by combining multiple drought mitigation mechanisms (Fig. 2), ensuring greater stability and efficacy across diverse agricultural systems.

Challenges/limitations

The performance of beneficial microbes for the mitigation of drought stress is significantly modulated by environmental factors such as soil characteristics, temperature, moisture, pH and native microbial communities; as a result, performance at the field level can often be inconsistent across regions and seasons (77). This makes the scaling up of microbial inoculants one of the key challenges in their progress from controlled experiments to field-scale applications, where scalability issues include those related to the maintenance of microbial viability, formulation stability and cost-effective production (78). Further, the high degree of strain-host specificity restricts the universal applicability of certain microbes against different crops and agro-ecological conditions. Other regulatory and biosafety concerns with respect to human health, the environment and the stability of ecosystems further complicate matters, with different standards existing across different regions (79). Commercial and intellectual property issues also stand in the way, since successful commercialisation needs sufficient field validation, technological investment, finance and effective management of patent rights. Academic institutions emphasise publication delays product development. Pathogenicity concerns for some endophytes pose an additional need for rigorous screening for toxin production and biosafety prior to deployment at large scales. Overall, complex plant-microbe-environment interactions and a lack of adequate field validation reflect a more urgent need for

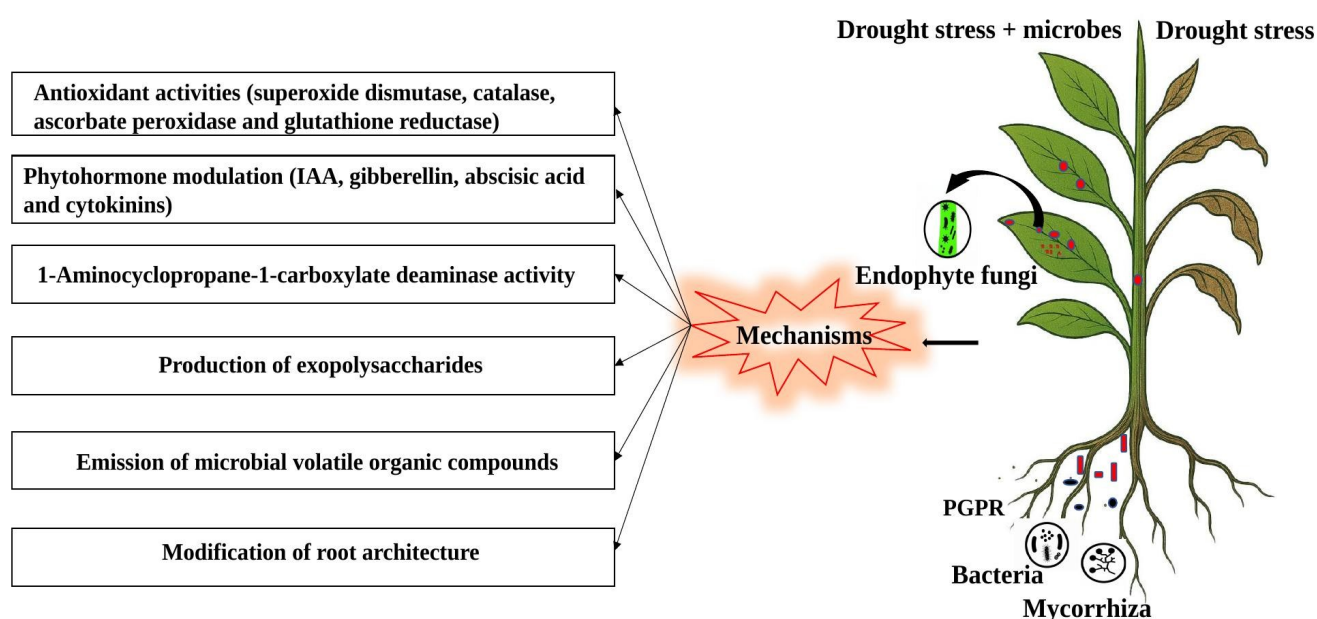


Fig. 2. Integrated role of different microbes in drought mitigation.

deeper mechanistic understanding and coordinated efforts toward ensuring the safe, scalable and effective application of microbial technologies to mitigate drought (80).

Conclusion

Beneficial microbes hold great promise for mitigating drought through the promotion of improved plant physiology, nutrient uptake and soil resilience; however, a lack of sufficient field validation, host-microbe specificity and instability of formulations have restricted their widespread adoption. The development of optimised microbial consortia, bio priming techniques, identification of stage-specific inoculation windows and standardisation of application methodology will bridge the gap between laboratory success and field application and will pave the way for scalable, microbe-based drought mitigation strategies.

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Authors' contributions

EKJJ, SA and CBK searched, collected and wrote the first draft. MA analysed the manuscript, provided the regular assistance to revise and finalise it. MA along with PSP and VSS reviewed and edited the manuscript. KNA critically reviewed and edited the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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