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LEGUME ROOT MICROBIOME INTERACTIONS UNDER CLIMATE: RESILIENT AGRICULTURE

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ABSTRACT

Climate change increasingly threatens legume production through recurrent drought and other environmental stresses, necessitating sustainable strategies to improve crop resilience. The legume root microbiome represents a dynamic interface between plants and soil and contributes to nutrient acquisition, biological nitrogen fixation, root development and stress adaptation. This review examines the composition and assembly of the legume root microbiome, focusing on rhizobia, arbuscular mycorrhizal fungi, non-rhizobial bacterial and fungal endophytes, and the role of root exudates in microbial recruitment. Particular emphasis is given to drought-induced changes in plant–microbe interactions and microbial mechanisms involved in water and nutrient acquisition, hormonal regulation, antioxidant defence, osmotic adjustment and maintenance of symbiotic nitrogen fixation. The potential of microbial inoculation, co-inoculation and microbiome engineering to enhance drought resilience in legumes is also discussed. Future integration of multi-omics, root phenotyping and field validation can facilitate the identification of stable and functionally effective microbial associations. Harnessing the legume root microbiome offers a promising approach for sustainable and drought-resilient legume production.

***Key words*:** Legumes, Root microbiome, Drought stress, Plant–microbe interactions,Microbial inoculation

Introduction

Climate change increasingly threatens agricultural productivity through recurrent drought, rising temperatures, salinity and erratic rainfall, necessitating agricultural systems that sustain productivity while enhancing resilience and reducing environmental impacts (Umkulzhum *et al*., 2024). Climate-smart agriculture (CSA) provides an integrated framework for improving productivity and adaptation while contributing to climate-change mitigation (Katel *et al*., 2022). Within this framework, the root microbiome has emerged as an important biological component supporting nutrient cycling, plant growth and crop resilience under changing environmental conditions (Purohit *et al*., 2024).

Legumes are important for climate-resilient agriculture because of their nutritional value and capacity for biological nitrogen fixation, which contributes to food security and soil fertility (Semba *et al*., 2021; Ciampitti *et al*., 2021; Pooja *et al*., 2023). Legume-based rotations and diversification can further improve soil fertility, nitrogen availability and carbon-related ecosystem functions (Matthews *et al*., 2025; Sharma *et al*., 2025). However, increasing climatic variability can adversely affect legume productivity and alter the microbial communities associated with their roots.

The root microbiome forms a critical interface between legumes and soil, comprising rhizobia and diverse bacterial and fungal communities that contribute to nutrient acquisition, phytohormone regulation, pathogen suppression and stress tolerance (Quides and Atamian, 2021). Root exudates, including sugars, amino acids, organic acids and secondary metabolites, regulate microbial recruitment and community assembly, while microorganisms reciprocally influence plant growth and

stress responses through metabolites, hormones and signalling mechanisms (Liu *et al*., 2016). Thus, plant–microbiome interactions constitute a dynamic communication network linking environmental conditions with microbial functioning and plant performance.

Climate stress, particularly drought, can disrupt these interactions by altering root physiology, exudation, microbial abundance and community structure, with consequences for nutrient acquisition and plant stress mitigation. Beneficial microbial inoculants and engineered microbial communities therefore offer opportunities to strengthen plant–microbe associations and improve drought resilience. However, the mechanisms linking root exudation, microbial recruitment, functional traits and plant responses remain incompletely understood. This review examines the composition and assembly of the legume root microbiome, with particular emphasis on its role in drought adaptation and the potential of microbiome-based approaches for developing climate-resilient legumes.

Legume Root Microbiome and Its Assembly

Major Bacterial and Fungal Groups

- **Rhizobia:**

Rhizobia are among the most functionally distinctive members of the legume root microbiome owing to their ability to establish symbiotic associations with legumes and fix atmospheric nitrogen. The establishment of an effective symbiosis involves two closely coordinated processes: rhizobial infection and subsequent nodule organogenesis (Oldroyd *et al*., 2011). Under nitrogen-limiting conditions, legume roots release flavonoids into the rhizosphere, which are perceived by compatible rhizobia and induce the synthesis of nodulation (Nod) factors. These signals activate host symbiotic signalling pathways and facilitate bacterial entry through infection threads formed in root hairs (Wang *et al*., 2018). Within developing nodules, rhizobia differentiate into bacteroids capable of reducing atmospheric N, to ammonia, thereby supplying the host with a readily assimilable nitrogen source. In return, the plant provides carbon compounds derived from photosynthesis to support bacterial metabolism (Oldroyd *et al*., 2011).

In addition to biological nitrogen fixation, rhizobia can contribute to plant growth and nutrient acquisition through several complementary functions, including indole-3-acetic acid (IAA) production, phosphate, zinc and potassium solubilization, siderophore production, and suppression of soil-borne pathogens through antimicrobial metabolites (Ahmad *et al*., 2013). However, the effectiveness of rhizobial symbiosis is influenced by the competitiveness and functional efficiency of the bacterial strain, host genotype, and prevailing soil and environmental conditions. These factors can result in considerable variation in symbiotic performance and may partly explain the inconsistent responses observed following the application of commercial rhizobial inoculants under field conditions.

- **Arbuscular Mycorrhizal Fungi (AMF):**

Arbuscular mycorrhizal fungi constitute the second major, evolutionarily ancient component of the legume root microbiome, so widespread and foundational that Parniske (2008) described the AM symbiosis as the ‘mother of plant root endosymbioses’. AMF colonize the root cortex and differentiate into highly branched intracellular structures called arbuscules, which serve as the principal interface for bidirectional nutrient exchange, the fungus supplies phosphorus and other soil-derived nutrients while receiving up to a fifth of the plant photosynthetically fixed carbon in return (Parniske, 2008). As their extraradical hyphal network extends well beyond its own root absorption zone, AMF substantially expand the effective volume of soil a legume can exploit for nutrient capture.

- **Non-Rhizobial Endophytes:**

Bacterial endophytes - In addition to rhizobia, legume nodules and roots host abundant non-rhizobial endophytic bacteria that do not themselves induce nodulation but contribute a wide range of plant growth-promoting (PGP) functions. A comprehensive systematic review of nodule-associated bacterial communities across multiple legume hosts identified *Bacillus* and *Pseudomonas* as the consistently dominant non-rhizobial genera, followed by *Paenibacillus*, *Enterobacter*, *Pantoea*, *Agrobacterium* and *Microbacterium*, with soybean, mung bean, common bean and lentil serving as the most extensively studied hosts (Hnini and Aurag, 2024). Among these, *Bacillus* is of particular applied interest for its capacity for IAA (auxin) biosynthesis, phosphate solubilization and siderophore production, along with its ability to enhance plant growth through induced systemic resistance, antibiosis and competitive exclusion of pathogens, aided by its characteristic ability to form stress-resistant spores that persist in harsh soil environments (Singh and Pujari, 2022). A key biochemical mechanism underlying such growth promotion in *Bacillus* and other PGP bacteria is production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which lowers stress-induced ethylene accumulation in host tissue and thereby alleviating growth inhibition under flooding, drought, salinity, pathogen attack and heavy-metal exposure and promoting nodulation itself (Glick, 2014). Related *Bacillus* species, including *B. thuringiensis*, have similarly been

shown to carry multiple PGP determinants simultaneously ACC deaminase, siderophore biosynthesis genes, phosphate solubilization and IAA production within single strains, indicating that individual *Bacillus* isolates can combine several growth-promoting mechanisms at once (Raddadi *et al*., 2008).

On the fungal side, fungal endophytes like *Piriformospora indica* (reclassified as *Serendipita indica*) is the best-characterized non-mycorrhizal root endophyte with proven growth-promoting and stress-alleviating effects (Adarsh *et al*., 2024). First isolated from the Thar Desert of northwestern India, it is distinguished from true AMF by its ability to grow axenically in culture while still replicating many AMF-like benefits, including enhanced drought tolerance (Mani and Ameena, 2022), and induction of both localized and systemic resistance to pathogens (Singh and Pujari, 2022). Colonization by *P. indica* alters host phytohormone profiles including auxin, ethylene, jasmonic acid, gibberellin, abscisic acid and salicylic acid thereby stimulating root proliferation and activating oxidative-stress defence pathways (Qiu *et al*., 2023). In legumes specifically, *P. indica* colonization of *Medicago truncatula* significantly increased biomass under severe salinity stress, an effect linked to elevated antioxidant enzyme activity, reduced malondialdehyde accumulation, and lower sodium ion content and electrolyte leakage relative to non-colonized plants (Alikhani *et al*., 2017). Beyond *P. indica*, legume root nodules have also been reported to harbour other fungal genera including *Aspergillus*, *Penicillium*, *Trichoderma*, *Fusarium* and *Rhizoctonia* recovered through culture-based isolation, though their functional roles within the nodule environment remain far less studied than those of bacterial endophytes.

Collectively, rhizobia, AMF, and non-rhizobial bacterial and fungal endophytes together form an interacting, multi-partner microbial community in legumes rather than a set of independent associations. Nitrogen-fixing symbionts, phosphorus-mobilizing fungi, and growth-promoting endophytes such as *Bacillus* and *Piriformospora indica* jointly shape legume nutrition and stress resilience which is explored further in the sections that follow detailing on root exudation and microbiome assembly.

- **Root exudates and microbial recruitment**

Root exudation represents one of the major mechanisms through which legumes influence microbial recruitment and microbiome assembly. Roots are active participants in below-ground interactions through the release of chemically diverse compounds into the surrounding soil. These root exudates include sugars, amino acids, organic acids, phenolics, flavonoids, volatile compounds, proteins and mucilage, which provide both nutrients and signalling molecules for rhizosphere microorganisms (Ma *et al*., 2022). The enrichment of readily available carbon compounds in the rhizosphere favours microorganisms capable of rapidly utilizing these substrates, resulting in a microbial community that differs from that of bulk soil (Ling *et al*., 2022). In this way, the bulk soil acts as an important microbial reservoir, whereas selective root exudation and rhizosphere conditions determine which members of this microbial pool become enriched around the roots (Hamonts *et al*., 2018).

Root exudates also function as chemical signals that regulate specific plant microbe interactions. In legumes, flavonoids released from roots initiate communication with compatible rhizobia and stimulate Nod-factor production, thereby contributing to rhizobial recruitment and nodule formation (Oldroyd *et al*., 2011). Similarly, Akiyama *et al*., (2005) demonstrated that strigolactones released by plant roots stimulate interactions with AMF. Beyond these specialized symbioses, sugars, amino acids and organic acids can act as chemo-attractants and support microbial colonization, while phenolics and flavonoids can selectively influence microbial growth and community composition (Sugiyama and Yazaki, 2014). Consequently, root exudation provides a mechanism by which plants can enrich beneficial microorganisms such as rhizobia, *Bacillus*, *Pseudomonas* and mycorrhizal fungi within the rhizosphere.

The composition of root exudates is dynamic and varies with plant genotype, developmental stage, nutritional status and environmental conditions. Chaparro *et al*., (2013) demonstrated that changes in root exudate composition during plant development were closely associated with corresponding changes in the functional capacity of the rhizosphere microbiome. Similarly, (Feng *et al*., 2021) emphasized that genotype, developmental stage and plant physiological status influence the composition of root exudates. Under stress conditions, alterations in exudation may selectively recruit microorganisms capable of improving plant adaptation, a process often described as a plant 'cry-for-help' response (Liu *et al*., 2024). Thus, root exudates act not only as carbon sources but also as ecological signals linking plant physiological status with the assembly and functioning of the root microbiome.

Factors shaping the legume root microbiome

Host genotype:

Host genotype is an important determinant of root microbiome composition because genetic differences

influence root architecture, nutrient acquisition, immune responses and the production of root-derived metabolites. Chaparro *et al*., (2013) demonstrated that soil type strongly influenced the composition of root endophytic communities, while plant genotype contributed additional selective effects on the microbial assemblage. More specifically, Brown *et al*., (2020) showed that host genetic factors were particularly important in determining microbial communities inhabiting the root endosphere and nodules of *Medicago truncatula*. These findings indicate that legumes do not passively acquire microorganisms from soil; rather, host genetic characteristics influence microbial recruitment and selection.

Plant developmental stage:

The root microbiome changes continuously during plant development as root physiology, nutrient demand and exudation patterns change. During germination, seed-derived compounds establish the spermosphere, which represents the first interface between the developing plant and soil microbiota. Schiltz *et al*., (2015) reported that compounds released from germinating seeds, including amino acids, fatty acids, phenolics and volatile compounds, influence the microbial community developing around the emerging radicle. As plants progress through subsequent developmental stages, changes in root exudation lead to corresponding changes in microbial community composition. For example, Aulakh *et al*., (2001) observed stage-dependent changes in rice root exudation, while Chaparro *et al*., (2013) demonstrated that changes in sugars, sugar alcohols, amino acids and phenolics during plant development were associated with changes in microbial functional genes. Therefore, developmental transitions provide a temporal framework for microbiome assembly, with different microbial communities being favoured at different stages of plant growth.

Soil physicochemical properties:

Soil represents the primary microbial reservoir from which root-associated communities are recruited, making soil physicochemical properties important determinants of microbiome assembly. Among these properties, soil pH is consistently identified as one of the strongest drivers of bacterial community composition. Fierer and Jackson (2006) demonstrated a strong relationship between soil pH and bacterial diversity across continental-scale soil samples, while Griffiths *et al*., (2011) confirmed a similar relationship across different spatial scales in Great Britain. In soybean rhizospheres, Zhang *et al*., (2018) identified soil pH as a major predictor of the geographical distribution and co-occurrence patterns of rhizosphere bacterial communities. Soil type can also exert persistent effects on microbial communities; Schreiter *et al*., (2014) found distinct microbial assemblages associated with different soil types even under comparable climatic and cropping conditions. Other properties, including organic carbon, nutrient availability, moisture and soil texture, further modify the microbial habitat and determine which microorganisms are able to establish in the rhizosphere.

Environmental stress:

Environmental stresses act as ecological filters that modify both the microbial community and the plant processes involved in microbiome recruitment. Drought is particularly important as beneficial microorganisms can alter root growth and nutrient acquisition under water limitation stress in rice (Mani *et al*., 2023a). Naylor and Coleman-Derr (2018) reported that drought can induce stronger shifts in rhizosphere microbial communities than in bulk soil communities because rhizosphere microorganisms experience both soil water limitation and stress-induced changes in the host plant. Under drought, relatively fast-growing bacterial groups may decline, whereas stress-tolerant groups belonging to Actinobacteria and Firmicutes can become enriched (Fuchslueger *et al*., 2016). In wheat, Breitkreuz *et al*. (2021) demonstrated that drought, soil type and farming system jointly influenced rhizosphere microbiome structure and functional capacity. Furthermore, Tiziani *et al*., (2022) showed that drought and heat stress altered root exudate profiles and were associated with the enrichment of specific microbial taxa. Such stress-induced restructuring of the microbiome may favour microorganisms capable of improving nutrient acquisition, hormone regulation and plant stress tolerance.

Drought stress:

Drought is a major abiotic constraint to legume production, particularly in environments characterized by prolonged or recurrent water deficits. Its effects can occur throughout the crop life cycle, from germination and seedling establishment to flowering, pod development and seed filling, with the magnitude of damage determined by the intensity, duration and developmental stage at which stress occurs (Khatun *et al*., 2021). Water limitation initially restricts germination and seedling establishment by interfering with enzymatic processes, reserve mobilization and energy production (Muscolo *et al*., 2014). As drought progresses, reductions in soil moisture alter plant water relations, stomatal behaviour, nutrient acquisition and photosynthetic activity, followed by oxidative and osmotic stress (Jabin *et al*., 2026). These effects can become particularly severe during reproductive development, when impaired flower and pod

formation and shortened seed-filling duration substantially reduce seed yield (Farooq *et al*., 2017). In legumes, drought responses therefore involve a coordinated adjustment of physiological, biochemical and developmental processes, together with interactions with root-associated microorganisms that can contribute to stress adaptation.

Drought-induced physiological and biochemical responses in legumes:

Drought stress rapidly alters plant water relations and stomatal behaviour. As soil moisture declines, stomatal closure reduces transpiration and conserves water, but simultaneously restricts CO_2 diffusion and photosynthetic carbon assimilation (Buckley, 2019; Asargew *et al*., 2024). Stomatal responses may also be initiated through hydraulic signals associated with rhizosphere drying and declining root–soil hydraulic conductivity (Abdalla *et al*., 2022; Cardoso *et al*., 2025; Bert *et al*., 2026). Declining soil moisture further restricts root water uptake and nutrient acquisition by reducing hydraulic conductivity, nutrient mobility and transport towards roots (Khatun *et al*., 2021). Consequently, reductions in leaf water and osmotic potential and relative water content disturb cellular hydration and turgor, while osmotic adjustment helps maintain cellular water status, with its effectiveness varying among legume genotypes (Ma *et al*., 2020; Noor *et al*., 2024).

Prolonged drought imposes both stomatal and non-stomatal limitations on photosynthesis. In addition to reduced CO_2 availability, water deficit can impair electron transport, promote photoinhibition, accelerate chlorophyll degradation and reduce photosynthetic capacity through reductions in leaf area and chlorophyll content (Thapa *et al*., 2011; Qiao *et al*., 2024; Wang *et al*., 2025). The resulting imbalance between light absorption and carbon assimilation favours excessive generation of reactive oxygen species (ROS). At controlled concentrations, ROS function as signalling molecules, whereas their excessive accumulation causes oxidative damage to lipids, proteins, nucleic acids and cellular membranes (Lee and Kim, 2024; Khatun *et al*., 2021). Plants counteract this oxidative stress through enzymatic antioxidants such as superoxide dismutase, catalase and ascorbate peroxidase, together with non-enzymatic antioxidants including ascorbic acid, tocopherols, carotenoids, phenolics and flavonoids (Nadeem *et al*., 2019; Foyer and Kunert, 2024). Enhanced antioxidant activity has been associated with drought tolerance in pea, chickpea, soybean and lentil (Osman, 2015; Guler and Pehlivan, 2016; Sinha *et al*., 2018).

Osmotic adjustment provides an additional mechanism for maintaining cellular hydration through the accumulation of compatible solutes such as proline, amino acids, carbohydrates and sugar alcohols (Mani *et al*., 2024; Iliæ *et al*., 2025). Proline acts as an osmoprotectant and also contributes to redox regulation, cellular protection and stress signalling (Hussain *et al*., 2019; Haghpanah *et al*., 2024). Accumulation of osmolytes has been reported in drought-stressed cowpea, lentil and chickpea, although the magnitude and predominant compounds vary among species and genotypes (Sinha *et al*., 2018; Priya *et al*., 2025). These physiological and biochemical disturbances ultimately result in reduced cell expansion, plant height, leaf area and biomass, along with leaf rolling, wilting and abscission (Thapa *et al*., 2011; Nadeem *et al*., 2019). In legumes, drought can additionally disrupt source–sink relationships and suppress symbiotic N, fixation, thereby limiting carbon and nitrogen availability (Ferguson *et al*., 2019; Rubia *et al*., 2025).

The reproductive phase is particularly vulnerable to water deficit. Drought during flowering and pod development can accelerate flowering, shorten the seed-filling period, impair gametogenesis and reduce pollen fertility (Farooq *et al*., 2017). Reduced photosynthetic carbon supply consequently restricts flower and pod development and may increase pod abortion because of inadequate assimilate availability and reduced sink strength (Poudel *et al*., 2025). The magnitude of yield reduction varies with legume species and developmental stage; drought during vegetative and reproductive growth has been associated with yield losses of approximately 70 per cent in cowpea, while podding-stage stress has caused reductions approaching 80 per cent in chickpea and substantial losses in lentil (Nunes *et al*., 2022). Thus, maintenance of water status, photosynthetic activity, antioxidant defence and reproductive function is fundamental to improving drought tolerance and minimizing yield losses in legumes.

Drought-induced changes in legume microbe symbioses:

The effects of drought are not restricted to plant physiological processes but also extend to the interactions between legumes and their root-associated microbial communities. Legumes form important associations with rhizobia, nodule-associated non-rhizobial bacteria (NRB) and arbuscular mycorrhizal fungi (AMF), which contribute to nutrient acquisition, growth promotion and stress adaptation (Álvarez-Aragón *et al*., 2023; Hu *et al*., 2022). Water deficit can alter root and rhizosphere conditions and consequently influence the establishment, activity and functioning of these microbial associations. At the same

time, changes in root physiology and exudation under drought can modify microbial recruitment and community composition, creating a dynamic interaction between plant stress responses and the root microbiome.

Among these interactions, rhizobial symbiosis is particularly important because biological N, fixation is highly sensitive to water deficit. Drought can suppress nodule formation, development and activity through changes in root and nodule water status, oxygen diffusion, rhizobial metabolism and nitrogenase activity (Iqbal *et al*., 2022). Since N, fixation requires considerable carbon and energy, drought-induced reductions in photosynthesis and carbon transport can limit the resources available for bacteroid respiration, nitrogenase activity and ammonium assimilation (Petrushin *et al*., 2023; Rubia *et al*., 2025). The extent of this response depends on host genotype, developmental stage and rhizobial strain, as microbial strains differ in their drought tolerance, nodulation competitiveness and capacity to maintain N, fixation under water-limited conditions (Ji *et al*., 2017; del-Canto *et al*., 2023).

Prolonged drought can also accelerate nodule senescence through oxidative stress, redox imbalance and alterations in defence-related signaling, leading to a progressive decline in nodule functionality and N, fixation capacity (Berrabah *et al*., 2024; Silva *et al*., 2024). Delaying drought-induced nodule senescence may therefore be important for sustaining nitrogen acquisition during prolonged stress. Nodule-associated NRB can potentially contribute to this process by influencing phytohormone balance, mineral nutrient availability and nodule functioning, thereby supporting effective rhizobial symbiosis under adverse conditions (Etesami and Santoyo, 2025).

AMF represent another important microbial component contributing to drought adaptation in legumes. Their extensive extraradical hyphal networks can explore soil beyond the root depletion zone and facilitate the acquisition of water and relatively immobile nutrients, particularly phosphorus documented in other crops (Hu *et al*., 2022; Subhash *et al*., 2025). Mycorrhizal associations can also contribute to improved soil aggregation and water retention, thereby creating a more favourable rhizosphere environment during soil drying. The complementary functions of rhizobia, nodule-associated bacteria and AMF therefore provide multiple pathways through which the legume root microbiome can support plant performance under drought (Duan *et al*., 2024).

Microbiome-mediated regulation of drought stress responses:

Beneficial microorganisms can enhance drought tolerance through interactions with plant hormonal signalling, root development, antioxidant defence and osmotic regulation. Drought perception involves hydraulic and cellular signals, including changes in cytosolic Ca^{2+} and reactive oxygen species (ROS), which activate downstream signalling pathways involving abscisic acid (ABA), jasmonates, ethylene, salicylic acid (SA), auxins, cytokinins and gibberellins (Takahashi *et al*., 2020). ABA acts as a major regulatory hub by promoting stomatal closure and stress-responsive gene expression through the PYR/PYL/RCAR–PP2C–SnRK2 pathway, although drought adaptation depends on interactions among multiple hormonal pathways (Ahmad *et al*., 2023; Chhaya *et al*., 2021; Shaffique *et al*., 2023). Root-associated microorganisms can modify these hormonal networks through microbial metabolites and plant-growth-promoting activities. In particular, ACC deaminase-producing bacteria reduce the availability of the ethylene precursor ACC, thereby moderating excessive ethylene accumulation, supporting root growth and alleviating drought-induced growth inhibition (Alemneh *et al*., 2020; Gamalero and Glick, 2025). Microbial auxin production can further promote lateral root development and root elongation, enhancing soil exploration for water and nutrients (Chhaya *et al*., 2021).

Microorganisms can also modify the rhizosphere environment through extracellular polymeric substances and biofilm formation, which support microbial colonization under declining soil moisture. Root endophytes such as *Piriformospora indica* can further promote root development and nutrient acquisition, supporting plant water relations when drought restricts nutrient diffusion and transport (Mani *et al*., 2023b). Beneficial bacteria and fungi may additionally stimulate plant antioxidant systems, enhancing ROS detoxification and reducing oxidative damage to membranes and photosynthetic structures. Microbial interactions can also promote the accumulation of proline and other compatible solutes, thereby supporting osmotic adjustment, cellular hydration and metabolic stability (Chhaya *et al*., 2021; Ahmad *et al*., 2023). Thus, microbiome-mediated drought tolerance involves coordinated regulation of root development, water and nutrient acquisition, hormonal signalling, ROS homeostasis and osmotic adjustment.

In legumes, these microbial effects are closely linked with symbiotic N, fixation, as ABA, ethylene and cytokinins regulate nodule initiation, activity and senescence (Berrabah *et al*., 2024). Microorganisms capable of sustaining root growth, moderating stress-induced ethylene, improving nutrient availability and maintaining nodule functionality may therefore provide

greater drought resilience than those acting through a single mechanism. The integration of microbial functions with plant signalling and symbiotic processes consequently represents an important basis for microbiome-mediated drought tolerance in legumes.

Microbial inoculation and microbiome-based drought mitigation:

The functional contribution of beneficial microorganisms to drought tolerance provides a basis for developing microbial inoculation strategies for legume production. *Rhizobia*, plant-growth-promoting bacteria, nodule-associated bacteria, AMF and fungal endophytes have been explored for their potential to improve plant performance under water deficit. Microbial inoculation can enhance nutrient acquisition, stimulate root development, regulate stress-related hormones and strengthen antioxidant defence, thereby reducing the negative effects of drought on plant growth and productivity (Saikia *et al*., 2018; Alemneh *et al*., 2020).

The use of microbial combinations is particularly promising because different microorganisms can provide complementary functions. R*hizobi*a contribute biological N_2 fixation, AMF improve access to water and phosphorus, while beneficial bacteria and fungal endophytes may promote root growth, regulate hormonal responses and strengthen stress defence. Such functional complementarity may be advantageous under drought because water deficit simultaneously affects plant water status, nutrient availability and symbiotic performance (Duan *et al*., 2024). Consequently, co-inoculation and microbial consortia may offer broader benefits than the application of individual microorganisms, provided that the component strains are compatible and capable of establishing under the target environmental conditions.

Recent developments in microbiome engineering have expanded the scope of microbial approaches beyond conventional inoculation. Growth medium made with paddy soil: farmyard manure: coir pith compost in 1:1:1 ratio for *P. indica* colonisation resulted in superior seedling growth across all evaluated parameters compared with uninoculated control in rice nursery (Adarsh *et al*., 2025). Manipulation of root traits, root exudation and microbial community composition can potentially favour beneficial plant microbe associations and improve nutrient acquisition, stress resilience and symbiotic performance (Joshi *et al*., 2025; Chesneau *et al*., 2025). However, the success of microbial inoculation is influenced by host genotype, soil properties, climatic conditions, indigenous microbial communities and interactions between introduced and resident microorganisms. Therefore, the development of reliable microbiome-based approaches for drought-resilient legumes requires greater emphasis on strain host compatibility, microbial consortia, persistence of introduced microorganisms and validation under field conditions.

Overall, drought tolerance in legumes is governed by an integrated interaction between plant responses and the root-associated microbiome. Water deficit alters plant water relations, photosynthesis, nutrient acquisition, redox balance and reproductive development while simultaneously affecting rhizobial, nodule-associated and mycorrhizal interactions. In turn, beneficial microorganisms can improve root development, water and nutrient acquisition, hormonal regulation, antioxidant defence, osmotic adjustment and symbiotic N, fixation. Thus, targeted microbial inoculation, compatible microbial consortia and microbiome engineering represent promising approaches for enhancing the resilience and productivity of legumes under increasing water scarcity.

Future perspectives and translational challenges

High-throughput root phenotyping can link omics-based mechanisms with root architectural and performance traits under abiotic stress (Luo *et al*., 2019; Reni *et al*., 2025). Future studies should integrate multi-omics with field-based phenotyping to identify robust plant and microbial markers of drought and other climate stresses. This could enable targeted selection of beneficial microbial communities and their integration into crop improvement programmes, accelerating microbiome-based approaches for climate-resilient legume production.

Conclusion

The legume root microbiome is a dynamic resource for climate-resilient agriculture, shaped by host genotype, developmental stage, root exudation, soil properties, environmental stress and management practices. Beyond rhizobia and arbuscular mycorrhizal fungi, diverse bacterial and fungal endophytes contribute to nutrient acquisition, hormonal regulation, pathogen suppression and stress tolerance. Drought and salinity can alter microbial community structure by modifying root physiology and microbial recruitment, while beneficial microbes can enhance plant resilience through improved nutrient and water acquisition, rhizosphere modification, antioxidant defence and stress signalling. Future research should prioritize functional traits, host–microbe compatibility, microbiome stability and field validation under combined stresses.

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