Deciphering the plant microbiome to improve drought tolerance: Mechanisms and perspectives

Sajad Ali [a],[*],[1], Anshika Tyagi [a],[1], Suvin Park [a], Rakeeb A. Mir [b], Muntazir Mushtaq [c], Basharat Bhat [d], Henda Mahmoudi [e], Hanhong Bae [a],[*]

[a] Department of Biotechnology, Yeungnam University, Gyeongsan, Gyeongbuk 38541, Republic of Korea
[b] Department of Biotechnology Central University of Kashmir, Ganderbal 191201, India
[c] National Bureau of Plant Genetic Resources, New Delhi 1100012, India
[d] Department of Bioresources, University of Kashmir, Srinagar 190006, India
[e] Directorate of Programs, International Center for Biosaline Agriculture, Dubai, United Arab Emirates

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ABSTRACT

Plants being sessile are constantly challenged by numerous abiotic stressors that jeopardize their survival. Drought stress is a major constraint in sustainable agriculture that affects plant distribution, growth, and productivity. Plants use multidimensional adaptation tactics at cellular, molecular, and biochemical levels to combat drought stress. These adaptive strategies have been extensively studied, and a variety of drought-resistance genes have recently been discovered. However, translating this information from the laboratory to field conditions is still a major challenge. Hence, developing novel long-term and successful drought mitigation strategies is an important aim in agriculture, as it is critical to ensure food security. One such approach is to explore the plant microbiome, which has recently become a research frontier. Plant microbiome engineering is being examined as a new aspect of sustainable agriculture, with the potential to improve crop resilience to drought. Plants restructure their microbiome against drought stress by employing the "cry for help" strategy, which can both alleviate stress and can improve health and nutrition availability. Mechanistic insights into the complex feedback between microbes and plants during and after water stress are required to fully harness the potential of above- and below-ground microbiome. The use of high-throughput tools to investigate the ecological, biochemical, physiological, and molecular aspects of the plant microbiome under drought stress will improve our ability to improve the drought resilience of crops in the future. This review highlights recent findings on the impact of drought and related signaling in plants. We also discuss the function of the plant microbiome in drought resistance in plants, as well as possible future research directions. Furthermore, we discuss the roles of multiomics, synthetic microbial communities (SynComs,) and host-mediated microbiome engineering for developing drought-resilient microbial communities in sustainable agriculture. Finally, we assess the challenges encountered and make recommendations for future endeavors to extend plant microbiome applications from the lab to the field.

1. Introduction

In nature plants face numerous environmental stresses owing to their sessile lifestyle. These unfavourable factors negatively impact plant growth, productivity and their geographic distribution. Under field conditions, plants may face these stresses (e.g., drought, salinity, and

* Corresponding authors.
  E-mail addresses: sajadmicro@yu.ac.kr (S. Ali), hanhongbae@ynu.ac.kr (H. Bae).
[1] These authors contributed equally to this work.

pathogens) individually or in combination, which can have a devastating impact on crop productivity (Teshome et al., 2020). Among abiotic stresses, drought is considered as a major detrimental factor for poor yield and productivity in economically important crops resulting in huge economic losses and threatening food security (Zhang et al., 2022). Due to the increasing rate of climate change, there is a high probability of agricultural land becoming more exposed to drought stress (IPCC, 2007; and Li et al., 2009). Furthermore, approximately 50 % of all cultivable land is expected to be affected by drought stress by 2050 (Vinocur and Altman, 2005; Kasim et al., 2013). Similarly, an increase in drought frequency and intensity would affect approximately two-thirds of the global population (Naumann et al., 2018), endangering food security. The demand for water in aagriculture has risen dramatically in recent decades, accounting for more than two-thirds of global water consumption (Rost et al., 2008). Furthermore, owing to climate change, the water demand for agriculture is expected to double by 2050, while freshwater availability is expected to decrease by 50 % (Gleick, 2000). Over the last decade, drought has been a major setback for the global agriculture economy, resulting in a loss of \$− 37 billion in total crop production (FAO, 2018). Thus, it is critical to develop high-yielding plants that use water more efficiently than their current counterparts or to find alternatives that will ensure their survival under drought conditions.

Plants require sufficient water for growth, development, and reproduction, and water shortages limit plant growth (Gupta et al., 2020). Plants integrate a wide range of morphological, physiological, and molecular defense responses against drought which prevents water loss, maintaining cellular water content and water supply to vital parts (Gupta et al., 2020). Plants can also synthesizes an array of osmolytes or osmoprotectants such as prolines, soluble sugars, and betaine spermines, to maintain cell turgor pressure during prolonged drought stress. Plants also protect themselves from drought-induced reactive oxygen species (ROS) and other radicals owing to their efficient antioxidant system (Siddique et al., 2016; Kaur et al., 2021). Nevertheless, another important plant defense strategy against drought is the transcriptional and translational reprogramming of key genes and proteins involved in signal perception and transduction, transcription factors and upregulation of drought tolerant genes, all of which drive drought resilience (Fang and Xiong, 2015).

Over the past two decades, researchers have focused on transgenic approaches and molecular breeding tools to increase drought resilience in different crops (Oladosu et al., 2019; Qaim, 2020). For instance, various biotechnological tools, such as CRISPR/Cas, RNAi, and transgenics, have made significant contributions to improving drought-resilient traits in both model and crop plants, but their accessibility to farmers has been limited due to high costs, complexity, ethical considerations and toxicity concerns (Shanker and Maheswari, 2017; Qaim, 2020). In addition adaptive responses in plants are driven by complex genetic features involving several pathways, which have proven to be major impediments to long-term drought-tolerant crop improvement. Therefore, scientists continue to investigate innovative strategies to improve drought resistance for sustainable agriculture. Utilizing the potential of the plant microbiome is one such strategy, as it has numerous beneficial impacts, is environmentally friendly and economically effective, and can help plants withstand a variety of environmental challenges. Recently researchers have focused on decoding microbial communities to improve food production sustainability and new evidence suggests that plant microbiome also assist plants in dealing with a variety of stressors, including drought (Bender et al., 2016; Thirkell et al., 2017; Rubin et al., 2017). Indeed, the utilization of particular or tailored microbial consortia could give a long-term solution to not only to abiotic and abiotic stressors but also to future yield stability. In this review, we start with the consequences of drought on plants followed by drought signaling. Second, we look at how the plant microbiome can help plants cope with drought stress. Finally, we highlight current research efforts for microbiome

engineering in sustainable agriculture to build drought-resistant microbial communities.

2. Effect of drought stress on plants

Drought occurs in plants when the amount of available water in the soil is limited, or when water is constantly lost through transpiration or evaporation owing to climatic conditions such as rising temperatures, thereby endangering plants survival. Drought affects plant growth by inhibiting various morphological, physiological, and biochemical processes such as changes in leaf and root length, biomass photosynthesis, respiration, translocation, carbohydrate synthesis, nutrient metabolism, ion uptake, and growth promoters (Kapoor et al., 2020). Additionally, drought stress reduces the rate of carbon fixation by inhibiting metabolism or limiting CO_2 input into leaves (Apel and Hirt, 2004; Farooq et al., 2009b). Similarly, drought primarily inhibits the photosynthesis system by causing an imbalance between light capture and utilization, reducing Rubisco activity and the amount of photosynthetic pigments, inhibiting leaf area, and damaging the photosynthetic apparatus (Farooq et al., 2009a). Furthermore, drought lowers seedling vigor and affects germination by reducing water intake. Plants exposed to drought stress show the following unique phenotypic signs: wilting and yellowing, discoloration, and leaf burning (Ullah et al., 2017). Inside the host, drought stress leads to various biochemical changes, such as an excessive accumulation of ROS including $^1O_2$, O_2^-, and H_2O_2, which can damage various tissues and cellular constituents such as nucleic acids and other biomolecules, resulting in cell death or so-called programmed cell death (PCD) (Gill and Tuteja, 2010). Drought stress can also alter biogeochemical cycles, such as the nitrogen and carbon cycles, and can reduce the decomposition of organic matter, which can significantly reduce the uptake of water and minerals by the root system, thereby increasing soil fertility. For instance, drought-triggered decreasing in macronutrient absorption and translocation (K, N, P) are found in number of plants (Suriyagoda et al., 2014). Furthermore, drought stress also lowers cation (Ca^{2+}, K^+ and Mg^{2+}) absorption by roots by altering cation permeability and transport networks. The latter can also limit growth by inhibiting the activity of several critical enzymes that participate in nutrient digestion, uptake, translocation, and metabolism (Hussain et al., 2018). In plants, the most prevalent drought-related symptoms are leaf senescence and drooping, leaf rolling and brittleness, scorching and limp leaves, premature fall, etiolation, wilting, turgidity, flower sagging, and leaf yellowing (Khan et al., 2018; Ruehr et al., 2019). Many essential attributes representing plant water relations in plants include relative water content (RWC), leaf water potential, stomatal conductance, transpiration rate, leaf and canopy temperatures (Farooq et al., 2009a). These traits have been found to be significantly affected during drought stress in plants (Nayyar et al., 2006). However, water scarcity affects plants at all growth stages but causes maximum damage during critical growth phases, such as during the seed development stage or reproductive phase, thereby reducing seed size, number, and quality, which are primarily responsible for substantial yield losses (Queiroz et al., 2019). Further, we have shown how drought stress affects plants morphological, physiological, biochemical traits and as well as their adaptive responses. (Fig. 1). Various factors such as drought intensity, frequency, duration, soil variables, growth stages and conditions, and type of plant have a substantial impact on the overall effect and duration of drought-related symptoms in plants.

3. Drought signaling in plants

Drought stress is a widespread and serious concern in agriculture and food industries, as it interferes with growth stages and hastens plant senescence (Liu et al., 2016). Drought or water deficit is a biological term used to describe when plants do not receive adequate water (Jaleel and Llorente, 2009). Plants sense drought stress through the roots and
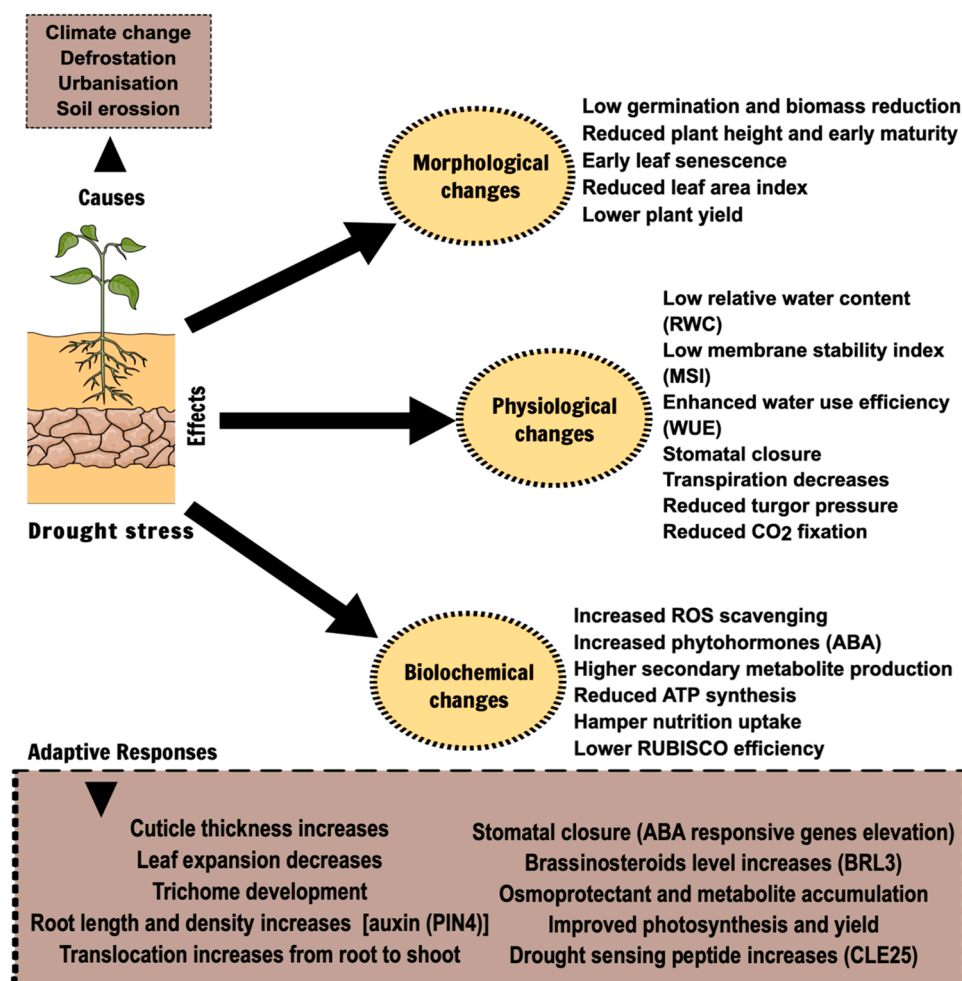
Fig. 1. Causes and effects of drought stress in the plant system. Schematic representation of hormone signaling modules, peptides, morphological and biochemical changes that are involved in drought adaptation.

stomata of their leaves and use inter-organ signaling to send water-deficient signals from roots to shoots. During drought stress, the first reactive step is that of signal perception, which is recognized by membrane-based receptors, followed by signal transduction and gene expression (Fig. 2). Drought induces oxidative, osmotic, and mechanical stress in plants, which are sensed by multiple sensors, such as ROS sensors, osmosensors, and Ca^{2+} channels. These intra- and inter-tissue or organ drought stress signals in plants are mediated by abscisic acid (ABA), phosphorylation, and diverse metabolites (Kuromori et al., 2022). In plants, various physiological signals like ABA, hydraulic, peptide, Ca^{2+} and ROS, are crucial players in modulating drought adaptive responses. Additionally, mitogen-activated protein kinases (MAPKs) and Ca^{2+}-dependent protein kinases (CDPKs) transduce drought signals to the nucleus by involving various TF regulons such as *DREB, MYB/MYC, NAC, ABRE,* and *WRKY*, which controls the expression of drought-tolerant genes (Fig. 2). In guard cells, increased accumulation of hydrogen peroxide (H_2O_2), a chief constituent of ROS, results in an increase in Ca^{2+} currents in response to ABA (Hamilton et al., 2000; Kuromori et al., 2022). Recently, the hydrogen-peroxide-induced Ca^{2+} increase (HPCA) has been identified as an H_2O_2 sensor in plant guard cells (Wu et al., 2020). In the short term, plants attempt to prevent water loss by regulating stomatal movement in leaves (Nakashima et al., 2014). Drought stress signaling is mediated by various factors, including hydraulic acid, K^+, Ca^{2+}, ROS, mRNA, and phytohormones (Christmann et al., 2007; Qi et al., 2018). For example, stress-induced apoplastic Ca^{2+} and ROS generated by annexin D4 (ANN4) and NADPH oxidase can also act as messengers to warn

neighboring cells to stress, a process known as cell-to-cell communication (Choi et al., 2017; Ma et al., 2019). The plasma membrane-located *Arabidopsis thaliana* histidine kinase 1/ Arabidopsis histidine kinase 1 (*ATHK1/AHK1*) mediates drought responses (Tran et al., 2007). Moreover, mobile peptides that act as messenger molecules in the vascular system are thought to aid plants in assembling distributed drought signals (Takahashi and Shinozaki, 2019; Takahashi et al., 2020). One peptide, named CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED25 (CLE25), which is mainly synthesized in roots, is a key component in long-distance dehydration communication from root to shoot, culminating in stomatal closure via regulation of ABA biosynthesis (Takahashi et al., 2018a).

In plant stress biology, phytohormones are the key factors that activate a large number of stress-responsive cellular pathways that define the overall status of plant survival during these conditions or make the host highly alert to other stresses. Among the phytohormones, ABA is widely known as a master drought signaling sensor from the root to the shoot (Chaves et al., 2003; Wang et al., 2009). ABA has multiple roles, ranging from signal perception from the environment to the adaptive mechanism by transcriptional activation or the regulation of a variety of biochemical, cellular, physiological, and developmental traits. Three primary receptors are known to perceive ABA- or drought-mediated signaling cascades in plants, such as PYR/PYL/R-CARs, GTGs, and CHLH/ABAR, which regulate various cellular processes such as stomatal closure, the reduction of transpiration rate, lipid metabolism, and various developmental processes, thereby increasing stress tolerance during drought. Drought signaling cascades in plants
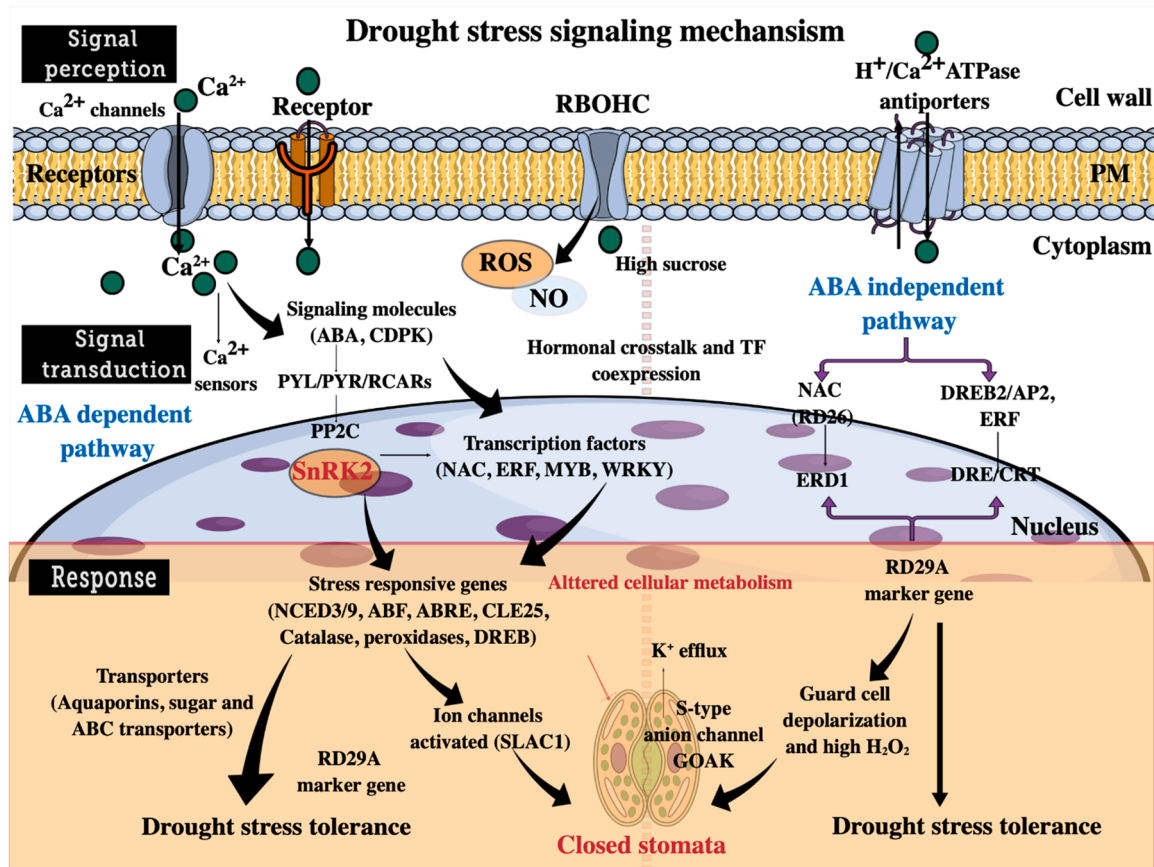
Fig. 2. A schematic diagram highlighting the signaling cascades and major signaling players involved in drought stress in plants. The first step of drought signaling is signal perception by cell wall receptors followed by calcium and ROS signaling. After signal perception, various players like calcium sensors, hormones (ABA, JA, SA, ET and other growth regulators), nitric oxide and transcription factors shown in the figure are involved in signal transduction. Ca^2 + -dependent protein kinases (CDPKs) and mitogen-activated protein kinases (MAPKs), ABA transduce drought signals to the nucleus by involving various TF regulons such as DREB, MYB/MYC, NAC, ABRE, and WRKY, which in turn regulate the expression of downstream genes linked to drought tolerance. This diagram also shows how numerous signaling molecules modulate adaptive responses during drought stress. Further, we have shown the adaptive response that is mediated by the ABA dependent and independent drought signaling pathways which modulate plant transcriptional and metabolic machinery, ion channels, and stomata closure for drought resilience.

function in both ABA-dependent as well as ABA-independent manner, involving similar and different signaling players. In addition, many genes that are involved in these distinct pathways have been identified in both model and crop plants, including ABA-binding factor (ABF), dehydration-responsive element-binding protein (*DREB*), *MYC, MYB,* and C-repeat-binding factor (CBF), and the stress-responsive cis-element ABA-responsive element (ABRE) and dehydration-responsive element (DRE) (Fig. 2). In general, plants facing desiccation initiate ABA accumulation, which acts as a regulator of stomatal closure. The interaction of ABA molecules with ABA receptor proteins, including PYR/PYL/R-CAR (pyrabactin resistance/PYR1-like/regulatory components of ABA receptors), initiates the ABA-dependent stomatal regulation pathway, followed by an activation of components in downstream signaling, PROTEIN PHOSPHATASES 2C (PP2C) and SNF1-RELATED PROTEIN KINASES 2 (SnRK2) (Gonzalez-Guzman et al., 2012). Generally, the PP2C is one of the key regulators of the ABA-dependent stomatal closure pathway, with subclass III SnRK2, such as SnRK2.6 (Mizoguchi et al., 2010). In detail, the trio-complex which is composed of ABA, ABA receptor, and PP2C, which inhibits the function of SnRK2.6 in the absence of ABA, frees SnRK2.6 to phosphorylate downstream genes, in addition to the S-TYPE ANION CHANNEL (SLAC1) and ABA-RESPONSIVE ELEMENT BINDING PROTEINS/ABRE-BINDING FACTORS (ARE-B/ABF), which are responsible for stomatal closure (Soma et al., 2021; Zhang et al., 2015). Additionally, ABA-dependent stomatal regulation of ABA also mediates ROS production by stimulating NADPH oxidases, which stimulate $[Ca^{2+}]_{cyt}$, resulting in guard cell stomatal closure (Pel

et al., 2000). Moreover, the vacuolar mechanosensitive K^+ channel, AtTPK1, directly controls the stomatal closure pathway by regulating the turgor pressure of vacuoles in guard cells, followed by the swelling of these cells (Isner et al., 2018). Although ABA is an important chemical in stomatal regulation, an ABA-independent stomatal closure pathway is activated early in the drought stress response (Nakashima et al., 2014). It is well documented that dehydration stress activates plant-specific transcription factors like (DREB proteins), which bind to DRE cis-elements and regulate ABA-independent stress-responses (Yoshida et al., 2014). Other key TF families that regulate ABA independent drought signaling pathways are ethylene-responsive factor (*AP2/ERF*), APETALA2, NAC, NAM and ATAF1/2 respectively (Takahashi et al., 2018b). Interestingly, under drought stress, NAC TFs regulates the expression of genes associated with ABA dependent as well as ABA independent pathways in plants. ABA-independent gene regulation during drought stress provides further evidence of the involvement of other phytohormones such as methyl jasmonates (MeJAs), salicylic acid (SA), ethylene (ET), cytokinins (CKs), auxins (AUX), gibberellins (GAs), and brassinosteroids (BRs). These small, versatile hormones can fine-tune the stress response and tolerance to drought stress either through synergistic or antagonistic interactions with ABA (Peleg and Blumwald, 2011). For example, MeJAs, such as ABA, cause stomatal closure by increasing pH and altering the amounts of ROS, nitric oxide, and Ca_2^+, which activate anion channels (Bharath et al., 2021). Previously, the primary role of SA in plants was thought to be the regulation of plant defense responses against pathogens however, SA also regulates

numerous abiotic stress signaling cascades including those induced by drought and salinity. For example, SA minimizes plant sensitivity to drought stress by controlling a variety of responses, including transpiration rates, stomatal movement, antioxidant defenses, and photosynthetic rates (Nazar et al., 2015). The exogenous treatment of SA improves drought resilience in plants by increasing the synthesis of dehydrin-like proteins, heat shock proteins, and chaperones, as well as by altering protein kinase activity, chlorophyll, and Rubisco concentration (Sun et al., 2009; Nazar et al., 2015). Besides JA and SA, ET also plays a key function in drought signaling in plants. For instance, various ETHYLENE RESPONSE FACTORS (ERFs) detect the DRE/CRT elements in stress-responsive genes, and either induce or inhibit their expression to regulate drought responses (Tiwari et al., 2012). In Arabidopsis, genetic data have revealed that ET biosynthesis and signaling gene knockouts modify plant sensitivity to ABA, which affects ABA-dependent drought tolerance (Dong et al., 2011). Under drought conditions, BR and AUX responses are linked to leaf and root growth through both ABA-dependent as well as ABA-independent modes (Gupta et al., 2020). CK is also involved in drought acclimation and adaptation as well as in plant yield stabilization during drought conditions (Li et al., 2016). Although these reports have emphasized the significance of many hormones and their cross-talk in drought signaling, further research is required to completely understand the molecular processes through which they balance the growth and stress response trade-offs under drought stress. Hydrogen sulfide (H_2S) and nitric oxide (NO) are key molecules that regulate drought stress in plants. For example, H_2S indirectly triggers guard cell movement by influencing secondary messenger signals, such as NO, H_2O_2, eATP, Ca^{2+}, phosphatidic acid (PA), carbohydrates, microfilaments, and microtubules, thus increasing stomatal closure during drought stress (Pantaleno et al., 2021). Similarly, NO has also emerged as an important player in drought signaling modulating a variety of processes including antioxidant system activity, osmolyte metabolism, and cross talk with ROS to fine tune drought-mediated downstream signaling pathways. Furthermore, NO may regulate Ca^{2+} (cGMP) and MAPK signaling pathways to minimize water loss via the ABA-induced stomatal response (Gayatri et al., 2013). Future research should concentrate on how NO and H_2S interact with other signaling players, as well as how they influence ABA-dependent as well as ABA-independent drought signaling in plants in order to better understand the complexities of drought signal perception and transduction. On the other hand, osmoprotectants, which act as ROS scavengers, which stabilize proteins and membranes and mediate cytoplasmic osmotic pressure, are generated and accumulate during drought stress (Saxena et al., 2013). Many osmoprotectants, including polyols (mannitol, sorbitol, and inositol), trehalose, proline, polyamine, ectoine, and glycine betaine, are important for the endurance of plant cells against drought (Saxena et al., 2013). Further, the schematic overview of the signaling cascades and key players involved in drought signaling in plants are shown in (Fig. 2). More mechanistic studies at the molecular level, such as genome editing approaches, are needed to functionally validate the genes involved in drought perception, signal transduction, and adaptation in crop plants.

4. Improving drought resistance in sustainable agriculture by harnessing the plant microbiome

Plants use multifaceted regulatory systems to deal with drought, such as drought tolerance, drought averting, and drought recovery as a part of the evolutionary process (Zhang et al., 2022). Drought tolerance mechanisms and the roles of numerous players have been comprehensively examined in recent years, and a variety of drought-tolerant gene pools have already been discovered in both model and non-model plants (He et al., 2019; Zhang et al., 2020). However, translating this information into crops with improved drought tolerance remains a most challenging task despite the development of novel scientific technologies. Stress biologists are at the helm of understanding the mechanism of

tolerance to drought stress, as this class of abiotic stress has multiple negative impacts on the biochemical and physiological attributes of crop plants, such as a reductions in ion uptake and translocation, the rate of respiration, the rate of photosynthesis, and the severe influence of CO_2 assimilation mechanisms (Naseem et al., 2018; Naylor and Coleman-Derr, 2018). Additionally, ROS production from the natural oxidative catabolism of oxygen is increased during drought, resulting in oxidative damage of lipids, carbohydrates, and proteins, culminating in membrane damage and necrosis (Bahadur et al., 2019). Despite several scientific studies describing various genetic engineering and molecular breeding approaches for improving drought resilience in crops, progress has been slow owing to the plant trait's complexity and the vast number of genes involved. As an alternative, crop plants can be primed to better handle drought stress. Chemical priming is currently used for drought mitigation in various crop systems that have been successful (Ali et al., 2019; Kaya et al., 2019). Numerous natural and synthetic chemicals, such as JA, SA, ABA, pipecolic acid, β-aminobutyric acid, azelaic acid hydrogen peroxide, and benzothiadiazole are used to prime plants for drought resilience (Savvides et al., 2016). Despite their involvement in stress resilience, chemical priming poses a threat to the ecosystem because of its capacity to react with other chemicals while also being more expensive. For example, plant ecosystems and microbiota are profoundly altered by the uncontrolled deposition of chemical compounds during chemical priming, which affects soil fertility and crop production (Lin et al., 2019). These significant drawbacks cast a disbelief on the widespread use of chemical priming in sustainable agriculture. Hence, new crop drought-resistance strategies that are both effective and environmentally friendly are urgently required. In this regard, harnessing the potential of the plant microbiome offers an alternative for improving drought resilience in sustainable agriculture, owing to its low-cost input and eco-friendly nature. Furthermore, the best features of plant microbiomes are their rapid growth, large population size, extreme physiological tolerance, high metabolic flexibility, and widespread dispersal in natural ecosystems, which make them unique and able to thrive in adverse environments (Jiao et al., 2019). Presently, this field is gaining momentum and much attention worldwide (Caddell et al., 2019; Liu et al., 2020). Plant-associated microorganisms help to improve soil structure, regulate pH, and improve oxygen and nutrient acquisition and transportation (Finkel et al., 2017). Microbial priming have long been known to aid crop development and stress resistance in a variety of ways, including nutrient acquisition through nitrogen fixation and insoluble mineral solubilization, siderophores, growth regulators, organic acids, and antimicrobial metabolites, all of these factors contribute to nutrient availability and stress mitigation. For instance, *Bacillus thuringiensis* AZP2 priming in wheat plants enhances their biomass and survival rate during drought (Timmusk et al., 2014). Similarly, the physiological and biochemical properties in okra are induced by biopriming with liquid phosphobacterium to ameliorate drought tolerance (Pravisya et al., 2019). Microbial bioinoculants (biopesticides, biofertilizers, bio-control agents, biostimulants and bioherbicides) are well known to improve nutrition and stress resilience in sustainable agriculture (Ahirwar et al., 2019). Due to the limitations of traditional bioinoculants, the attention has switched to more effective alternatives like harnessing plant microbiome for improving drought resilience in sustainable agriculture. Despite the huge benefits of microorganisms to plants, cultural limitations limit our ability to fully exploit the potential of the microbial world. Unfortunately, only a small fraction of the microbial world have been cultivated in under laboratory conditions (Tringe et al., 2005). It is unclear how much of the residual microbiome is actually uncultivable, and many more microorganisms will need to be isolated on growth conditions that better fit their dietary and metabolic needs. Nevertheless, the most significant influence on our understanding of microbiomes has come from culture-independent techniques based on DNA sequencing technologies. Over the last two decades, the advent of high-throughput tools and methodological breakthroughs have spurred plant microbiome

research, allowing the field to thoroughly examine theories offered over a century ago and to develop a slew of new possibilities (Fitzpatrick et al., 2020).

The last few decades have unraveled the critical role played by plant-associated microbiomes in maintaining plant growth and metabolism in terrestrial ecosystems and in positively responding to the rapidly changing dimensions of the environment. It is critical to obtain an in-depth knowledge of microbe-to-microbe, plant-to-microbe, or plant-to-microbe coordination to unravel the interlocking complexities of cross-kingdom relationships. Plant-associated microbiomes are valuable sources for protecting plants against stress and are promising living agents to pave the way for sustainable agricultural development (Ullah et al., 2019). For instance, plant and rhizosphere microbiomes interact in a variety of ways. Plants provide carbon (C) to the soil food web via subterranean C inputs. The rhizosphere microbiome, in turn, provides nutritional benefits to plants thereby regulates the balance of C respiration and soil stability. Furthermore, the rhizosphere microbiome also benefits plants through direct interactions such as infecting roots, developing symbiotic relationships, boosting plant growth as well as stress resilience by triggering or secreting different hormones (de Vries et al., 2020). Similarly, the phyllosphere or aerial surface of plants also harbor diverse microbial communities that help in improving host fitness by producing nutrients, phytohormones, and assisting with stress tolerance. Microorganisms penetrate and colonize internal plant tissues, forming the endospheric microbiome, which aids plants in a variety of ways, including growth promotion and stress resistance. In plants, the endosphere microbiome is generally less diverse than the exterior microbiome. Although plants develop resilience to drought through several phenotypic adaptations, several studies have revealed the instrumental role played by plant-associated microbiomes in enhancing drought tolerance (Farrar et al., 2014). Microorganisms use multifaceted defense systems at morphological, biochemical, and physiological levels (cell wall architecture morphology, exopolysaccharides (EPS)/biofilm formation, sporulation, osmoprotection) to survive drought stress. They also hold traits beneficial to their host plants by forming barriers such as EPS/biofilm formation or through modulators such as hormone production, osmoprotection, and antioxidant production, as well as nutrient and C acquisition and processing, which can help plants resist drought-mediated negative effects (de Vries et al., 2020). Under drought stress, plants modulate their growth and their associated microbiomes to alter nutrient cycling, such as changes in the dynamics of carbon (C) and nitrogen (N) cycling processes (de Vries et al. (2018; de Nijs et al. (2019). Plants rely heavily on plant-associated microbiomes to cope with drought stress (de Vries, Wallenstein, 2017, 2020; Cavicchioli et al., 2019). Several rhizosphere-associated microbial species have been found to enhance plant growth during drought stress through nitrogen fixation, nutrient solubilization and, secretion and stimulation of growth regulators, volatile organic compounds, organic acids, as well as many enzymes like ACC deaminase (Ahkami et al., 2017). The application of microbial communities enhances drought tolerance, the mobilization of nutrients, and the activation of growth-promoting traits (ALKahtani et al., 2020). Plant-associated microbiomes positively influence morphological traits, such as root length, secondary root growth, and the number of leaves, biomass, and phenological attributes such as flowering time, during stress (Table 1). Furthermore, we discuss how plant microbial community sustainability mitigates drought stress in plants as barriers and modulators.

4.1. Plant microbiome as emerging barrier for drought stress in plants

The plant microbiome is emerging as an important barrier or indirect layer of plant defense against biotic and abiotic stressors. Plants can modify and recruit beneficial microbial communities to survive in harsh environments. Plant-associated microbes are found to form a biofilm by the secretion of exopolysaccharides (EPS) or polymeric substances in pursuit of adhesion with plant roots. EPS has a high water-retention

Table 1
Microbiome induced resilience traits triggered in plants to mitigate drought stress.

Name of Plant species	Name of the host associated microbial strain/s	Drought tolerance traits imparted on host plant	References
Helianthus annuus (Sunflower)	*Rhizobium sp. strain YAS34*	✓ Increases dry biomass ✓ Increase RAS/RT ratio ✓ Enhances nitrogen uptake	Alami et al. (2000)
	Pseudomonas putida strain GAP-p45	✓ Aids soil aggregation to increase root adherence stability ✓ Leads to Biofilm formation on surface of root	Sandhya et al. (2017)
Zea mays L. (Maize)	*Proteus penneri Pseudomonas aeruginosa Alcaligenes faccalis*	✓ Enhances physiological attributes such as, root length, shoot length, leaf area and biomass ✓ Helps in improvement of soil moisture content	Naseem and Bano (2014)
	Bacillus amyloliquefaciens, B. licheniformis, B. thuringiensis, B. subtilis, Paenibacillus favisporus	✓ Enhances relative water content ✓ Increase RAS/RT ratio ✓ Increase soil aggregation stability ✓ Increases biomass	Khan et al. (2019)
	Burkholderia phytofirmans Enterobacter sp.	✓ Enhances physiological attributes such as, root length, shoot length, leaf area and biomass, photosynthetic efficacy and chlorophyll content	Naveed et al. (2014b)
Glycine max (soya bean)	*Bacillus licheniformis, B. megaterium, B. pumilus*	✓ Enhances overall plant growth	Susilowati et al. (2018)
	Sphingomonas	✓ Enhances phytohormone content such as, ABA and jasmonic acid ✓ Increased dry biomass in plants ✓ Enhances concentration of photosynthetic pigments, proline, glycine, glutathione and glutamine	Asaf et al. (2017);Khan et al. (2014)
Triticum aesativum L.	*Streptomyces coelicolor S. olivaceus S. geysiriensis*	✓ Enhances phytohormone content such as, auxin and IAA production ✓ Aids in higher seedling vigor as well as yield	Yandigeri et al. (2012)
	Pantoea alhagi	✓ Enhances production of siderophores, EPS, IAA, soluble	Chen et al. (2017)

Table 1 (*continued*)

Name of Plant species	Name of the host associated microbial strain/s	Drought tolerance traits imparted on host plant	References
		sugars, ammonia and protease production, ✓ Decreases chlorophyll degradation	
	Burkholderia phytofirmans	✓ Enhances photosynthetic rate, chlorophyll content and grain yield ✓ Increases water use efficiency, ✓ Maintains ionic balance and ✓ Improves antioxidant levels	Naveed et al. (2014a)
	Growth-promoting Rhizobacteria	✓ Enhances physiological attributes such as, vegetative growth, transpiration rate, photosynthetic rate, chlorophyll content, ✓ Improves internal CO_2 concentration, leaf water potential and stomatal conductance	Niu et al., 2020
	Bacillus sp.	✓ Aids soil aggregation to increase root adherence stability	Ashraf et al. (2004)
	Rhizobium sp.	✓ Aids soil aggregation to increase root adherence stability and increase in water holding capacity of soil in rhizosphere in plants	Kaci et al. (2005)
	Rhizobium leguminosarum *Mesorhizobium ciceri* *Rizobium phaseoli*	✓ Improves growth and biomass ✓ Improves overall drought tolerance index	Hussain et al. (2014)
	Rhizobium strain KYGT207	✓ Aids soil aggregation to increase root adherence stability	Kaci et al. (2005)
	Klebsiella sp. IG3	✓ Aids soil aggregation to increase root adherence stability and increase in water holding capacity of soil in rhizosphere in plants	Gontia-Mishra et al., 2016
	P. aeruginosa PM389 *P. aeruginosa ZNP1* *B.endophyticus J13* *B. tequilensis J12*	✓ Enhance production of phytohormones and EPS ✓ Enhance fresh weight and dry weight ✓ Increases water content	Ghosh et al. (2019)
Arabidopsis thaliana	*Pseudomonas chlororaphis O6*	✓ Help in reduction of stomatal	Cho et al. (2018)

Table 1 (*continued*)

Name of Plant species	Name of the host associated microbial strain/s	Drought tolerance traits imparted on host plant	References
		opening and wilting	
	Bacillus amyloliquefaciens FZB42	✓ Enhance fresh weight and dry weight ✓ Increase length of primary root ✓ Induces overexpression of drought defense-related genes, such as RD17, RD29A, ERD1, LEA14 ✓ Increase production of proline ✓ Enhances activities of enzymes such as, superoxide dismutase and peroxidase	Lu et al. (2018)
Lactuca sativa (Lettuce)	*Pseudomonas mendocina*	✓ Helps in promoting soil fertility as well as stabilization ✓ Aids soil aggregation to increase root adherence stability and increase in water holding capacity of soil in rhizosphere in plants ✓ Triggers increase in total carbohydrates	Kohler et al. (2006);Kohler et al. (2009)
Cicer arietinum (Chick pea)	*Bacillus subtilis*	✓ Increase production of proline ✓ Aids lipid peroxidation ✓ Enhances activities of antioxidant enzymes such as, APOX, CAT, POD, SOD	Khan et al. (2019)
	Rhizophagus irregularis	✓ Shoot length, root length and root density is improved ✓ Number of primary branches are increased	Hashem et al. (2018)
Setaria italica L. (Foxtail millet)	*Pseudomonas fluorescens*	✓ Efficiently colonized the roots ✓ Helps in soil aggregation to increase root adherence stability and increase in water holding capacity of soil in rhizosphere in plants	Niu et al. (2018)
Vitis (grapevines)	*Bacillus amyloliquifaciens*	✓ Enhances secretion of melatonin, ✓ Reduced concentration of H_2O_2, O2 − and MDA	Jiao et al. (2016)

Table 1 (*continued*)

Name of Plant species	Name of the host associated microbial strain/s	Drought tolerance traits imparted on host plant	References
Trifolium arvense (Hare's-foot clover)	*Pseudomonas azotoformans*	✓ Relative water content is increased ✓ Maintains higher chlorophyll content ✓ Enhances activities of CAT, SOD and POD ✓ Increase proline content ✓ Enhances plant biomass	Timmusk et al. (2014)
Saccharum officinarum (Sugarcane)	*Glucoacenatobacter diazotrophicus*	✓ Induced expression of drought stress responsive genes ✓ Activation of ethylene and ABA signaling pathways	Vargas et al. (2014)
Foeniculum vulgare (Fennel)	*Glomus intraradices*	✓ Increases leaf nutrients ✓ Regulates osmotic adjustment	Zardak et al. (2018)

competency which aids plant survival in drought conditions. EPS are a class of microbial exopolysaccharides consisting of high molecular weight polymers, which have proven solid for their role in resilience against a wide range of abiotic stresses, such as drought (Bhagat et al., 2021; Morcillo and Manzanera, 2021). Recent study have revealed that maize plants inoculated with EPS-producing bacteria increases photosynthetic rate, stomatal conductance as well as other physiological traits during drought (Naseem et al., 2018). Various bacterial species, including *Bacillus* sp., *Pseudomonas* sp., and *Rhizobium* sp., secrete EPSs that are critical for biofilm formation to aid the colonization of bacteria around roots and enhance plant drought resilience (Putrie et al., 2013). Furthermore, maize seeds primed with different bacteria (EPS-secreting) including *Pseudomonas aeruginosa, Alcaligenes faecalis* and *Proteus penneri* enhanced soil moisture content and plant growth traits shoot and root length, leaf area) as well as plant biomass (Naseem and Bano, 2014). For instance, capsular polysaccharides and EPS released by root-associated microbes alleviate drought stress by reducing water loss from roots, maintaining a hydrated microenvironment around the roots, and enhancing the survival of bacteria (Roberson and Firestone, 1992). The level of stress largely defines the complexity of EPS in terms of production and composition (Donot et al., 2012). For example, *Azospirillum brasilense* Sp245 secretes high molecular weight carbohydrates such as polysaccharide-lipid complexes and lipopolysaccharide-proteins under extremely arid conditions, which may aid bacteria and their companion plants in surviving (Konnova et al., 2001). Subsequently, the formation of EPS biofilms ensures a hydrated microenvironment to guarantee resilience to drought (Donot et al., 2012). Likewise, the *Pseudomonas putida* GAP-P45 strain secretes EPS, resulting in the formation of biofilms around the root surfaces of sunflower seedlings, promoting the aggregation of soil in the rhizosphere (Vardharajula 2009). The production of biofilms by bacteria improves plants' ability to endure drought by activating their metabolic adjustment dynamics. For instance, bacterial consortia including *B. subtilis*, *B. licheniformis*, and *B. amyloliquefaciens* secrete an EPS, which induces soil aggregation, enhancing seed germination and seedling growth in soybeans (Vardharajula 2014). Additionally, strains of EPS secreting *P. putida* form viable biofilms around the roots of sunflower and maize seedlings to enhance the soil holding capacity and improve the soil structure to mitigate drought stress. Similarly, Ali et al. (2014) reported that EPS

secreted by bacteria helps in the colonization of microbes around the root with the help of fibrillary material and regulates the diffusion of organic C sources as well as enhancing water retention under water stress conditions. Interestingly, supplementation with silica particles enhances EPS production and the subsequent formation of a biofilm, which in turn increases the osmotic pressure and water retention competency of the biofilm, and enhances root colonization, thus boosting plant growth features during under drought (Fetsiukh et al. (2021)). Most recently, Vardharajula (2021) reported that EPS production by strains of *Bacillus* spp. such as, HYD-B17, HYTAPB18, and RMPB44, helps in the aggregation of soil to enhance tolerance to drought stress. Additionally, EPS-producing bacterial strains such as *Pseudomonas fluorescens* FAP2 and *B. licheniformis* B642 produces an array of plant growth-promoting molecules such as IAA, ammonia and siderophores, which aid in phosphate solubilization. In addition they also modulate various biochemical and physiological parameters in plants during drought stress (Ali et al., 2014). Evidently, under drought stress conditions, plant-associated microbiomes improve plant metabolism and growth traits either by directly triggering the production of phytohormones and transport of nutrients or indirectly by synthesizing lytic enzymes, mediating pathogen suppression, and inducing systematic responses in plants (Ullah et al., 2019a; 2019b).

4.2. Microbes as modulators in plant drought stress resilience

Under drought, plant-associated microbiomes have been found to secrete diverse molecules, such as phytohormones, osmolytes, and antioxidants during drought which are the primary mechanisms by which microorganisms boost plant drought tolerance (Ullah et al., 2019a; 2019b). Phytohormones, such as IAA, cytokinin, gibberellins, ET, ABA, SA, JA, and BR, can help plants cope with abiotic stressors in addition to being essential for plant growth and development. The regulation or generation of phytohormones is one of the key processes by which plant microbial communities relieve stress and improve plant growth characteristics under drought. For example, PGPRs are known to improve crop growth during drought stress by modulating phytohormones, like ABA (Egamberdieva et al., 2017), cytokinins (Liu et al., 2013), IAA (Jochum et al., 2019), and by reducing ET formation (Belimov et al., 2015). Cohen et al. (2015) revealed that *Arabidopsis* treated with *A. brasilense* enhanced ABA synthesis to cope with drought stress. These studies also revealed that elevated levels of photosynthetic pigments, enhanced growth, and RWC were observed in *A. thaliana* during drought. Similarly, during drought, rhizobacteria increase the production of hormones like GA, IAA, SA, JA, CKs, and BR in sorghum plants, which plays a major role in drought resilience (Carlson et al., 2020). On the other hand, IAA-producing bacteria have been found to mediate drought and salt tolerance through diverse mechanistic stimulations, such as increasing the permeability of water, water uptake, detoxification of ROS, improvement in root architecture, as well as the induction of vast number of stress-resistant genes (Etesami and Maheshwari (2018); Ha-tran et al. (2021)). Similarly, wheat seedlings inoculated with different rhizobium strains produce IAA, which promotes drought resilience and improves growth and biomass during drought (Hussain et al., 2014). Further, inoculation of soybean plants with *Pseudomonas putida* H-2–3 improves drought tolerance by generating GA which modulates various growth and stress resilient features (Kang et al., 2014). Furthermore, Arabidopsis plants inoculated with *Phyllobacterium brassicacearum* strain STM196, increases ABA levels, which reduces leaf transpiration during drought stress (Bresson et al., 2013). According to Liu et al. (2013), inoculation of *Platycladus orientalis* with CK-producing *Bacillus subtilis* showed increased ABA concentrations, enhanced stomatal conductance as well as boost drought resistance. Plant-associated microbiomes enhance plant performance by modulating phytohormones to improve abiotic stress tolerance (Egamberdieva et al., 2017). Another major strategy employed by bacteria to enhance plant development during drought is the production of ACC deaminase, which cleaves ET

precursor ACC respectively. ET suppresses both shoot and root growth, which makes it difficult for plants to survive in drought circumstances. Inoculating crops with ACC deaminase-producing microorganisms has been proven in numerous studies to improve drought resistance and growth characteristics. For example, *Pisum sativum* inoculated with *Pseudomonas fluorescens* (ACC deaminase-producing) results in longer roots, which enhances the plants water intake capacity during drought conditions (Zahir et al., 2008). An endophyte, *Burkholderia phytofirmans* PsJN, supports plant growth by producing ACC deaminase and mutations of these bacteria that lack ACC deaminase activity are no longer capable of aiding root elongation in canola seedlings (Sun et al. (2009)). Exploring the plant microbiome for novel ACC-producing microbial strains appears to be more difficult because ACC deaminase is not present in all strains of a specific bacterial species. Remarkably, the synthesis of plant promoting substances such as IAA, GA, cytokinin phytohormones, and siderophores and the enhanced activity of ACC deaminase were observed upon investigating the role of bacterial root endophytes in maize plants (Sandhya et al., 2017). These findings emphasize the significance of the plant microbiome in drought stress mitigation by producing hormones or modulating plant hormonal signaling pathways. However, many questions remain unanswered: 1) How do microbes modulate hormonal cross-talk to balance growth and stress tolerance trade-offs? 2) How do microbes trigger hormonal signaling pathways either directly or indirectly? 3) How does microbial triggered hormone augmentation in plants affect root exudates for microbial survival under drought stress? 4) How do microbes modulate hormonal cross-talk in plants exposed to combined stressors like drought and salinity or infection and drought?

During drought stress, plants generate excessive amounts of different ROS, which causes oxidative damage to cells, such as membrane deterioration, increased lipid peroxidation, DNA fragmentation, protein degradation and eventually cell death. Plants, on the other hand, defend themselves by activating their antioxidant machinery (both nonenzymatic and enzymatic) to protect themselves from ROS damage and to maintain normal cellular function. Interestingly, plant antioxidant systems are modulated by the plant microbiome, which helps plants cope with drought stress. The plant microbiome plays an important role in alleviating drought stress by modulating plant enzymatic and non-enzymatic antioxidant systems. For example, the co-inoculation of basil plants with different bacterial species *viz., Bacillus lentus, A. brasilense* and *Pseudomonades* sp., resulted in increased APX and GPX activities as well as improved chlorophyll content during drought stress (Heidari and Golpayegani, 2012). Similarly, inoculating rice plants with *P. synxantha* and *P. jessenii* promotes its growth during drought by augmenting the activities of different antioxidants such as APX, POD, SOD, and CAT (Gusain et al., 2015). In addition, after being inoculated with *Bacillus firmus* and *Bacillus pumilus*, potato plants showed increased antioxidant activity, which increased drought tolerance (Gururani et al., 2013). However, several studies have indicated that microbially inoculated plants had lesser antioxidant activity than non-inoculated plants, implying that drought has a milder impact on inoculated seedlings. For instance, the inoculation of drought-resistant microbial strains *P. entomophila, P. syringae, P. stutzeri, P. montelli,* and *P. putida* in maize plants resulted in significantly lower antioxidant enzyme activities during drought stress than non-inoculated plants, indicating that drought stress has a lower impact on inoculated seedlings. However, under drought inoculated maize plants had more plant biomass, solutes, sugars, RWC, and leaf water potential than uninoculated maize plants (Sandhya et al., 2010). A subsequent study also showed similar findings in maize plants after inoculation with drought-tolerant bacterial strains, such as *B. licheniformis, B. amyloliquefaciens, B. subtilis, B. thuringiensis,* and *Paenibacillus favisporus* during drought stress (Vardharajula et al., 2011). Thus, the application of microbial communities significantly improves drought tolerance in plants by modulating their antioxidant systems.

Plants respond to drought-induced changes by producing numerous osmoprotectants (mannitol, proline, glycine betaine, trehalose) and ions which help with osmotic adjustment, the stabilization of subcellular structures, and free radical scavenging to combat the negative impacts of drought (Huang et al., 2014). Plant microbial communities produce various osmotically active molecules or ions that protect plants during drought stress conditions. For instance, the combination of plant-associated microbiomes derived from *Megathyrsus maximus* has been reported to improve drought resistance by accumulating proline, reducing the malondialdehyde content, and decreasing the activity of glutathione reductase (Moreno-Galván et al., 2020). Plant-associated microbiomes modulate proline expression under drought stress in plants. For example, cucumber plants inoculated with the microbial strains *B. subtilis* SM21, *B. cereus* AR156, and *Serratia* sp. XY21 augmented the proline content of their leaves by three to four fold, protecting them from dehydration during drought (Wang et al., 2012). Similarly, treatment of tomato plants by *B. polymyxa* improved drought tolerance by increasing osmolyte secretion (Shintu and Jayaram, 2015). In *Arabidopsis thaliana*, *P. putida* upregulates the transcript levels of genes involved in proline biosynthesis, resulting in increased water content, chlorophyll concentration, and plant biomass (Ghosh et al., 2017). High levels of glycine betaine and choline were found in maize plants after inoculation with *Raoultella planticola*, *Klebsiella variicola*, and *Pseudomonas fluorescens*, which boosted plant growth as well as drought resistance (Gou et al., 2015). Similarly, drought-stressed sorghum plants showed considerable osmotic adjustment and improvement in growth parameters after being inoculated with bacterial root endophytes such as Enterobacter sp., Microbacterium sp., and Ochrobactrum sp. (Govindasamy et al., 2020). Huang et al. (2017) also showed drought-stressed maize plants inoculated with *Burkholderia* sp. and *Mitsuaria* sp. modulated several physiological attributes, such as higher antioxidant activity, increased proline accumulation, phytohormone accumulation in leaves, and a lowering of the MDA content. Likewise, the combination of different microbial strains derived from *Megathyrsus maximus* are reported to enhance tolerance to drought by accumulating proline, lowering the malondialdehyde content, and decreasing the activities of glutathione reductase (Moreno-Galván et al., 2020). For instance, under drought stress, arbuscular mycorrhizal fungi (AMF) enhance water uptake and improve photosynthetic efficacy under osmotic stress (Bowles et al., 2018).

Microorganisms can also produce different volatile organic compounds (VOCs) which can help plants develop and cope with stress in both direct and indirect ways (Hashem et al., 2019). It is well documented that VOCs produced by beneficial microorganisms can activate a variety of defesne signaling responses, such as induced systemic resistance (ISR) and induced systemic tolerance (IST), which provide stress resilience in both below and above ground plant compartments. According to a recent study, VOCs produced by *Pseudomonas pseudoalcaligenes* improved numerous biochemical and physiological features in maize during drought stress, including increased proline and chlorophyll content, activated antioxidant enzymes, and reduced electrolyte leakage and MDA accumulation (Yasmin et al., 2021). Similarly, *A. thaliana* treated with *B. subtilis* (GB03) VOCs accumulate more glycine betaine as well as choline in response to osmotic stress than plants not exposed to VOCs, resulting in osmotic tolerance (Zhang et al., 2010). On the other hand, Arabidopsis plants treated with 2,3-butanediol (VOCs) or inoculated with *P. chlororaphis* O6 showed enhanced stress tolerance under drought circumstances, this was apparently because of reduced water loss and increased stomatal closure (Cho et al., 2008). Previous study have shown that VOCs like acetic acid can induce the biofilm formation which provides protection during drought stress. Hence, by promoting EPS synthesis, certain microbial VOCs may indirectly boost plant drought tolerance (Chen et al., 2015). Hence, examining the VOCs produced by plant microbiome during drought stress can open new avenues for mitigating drought stress in sustainable agriculture. Furthermore, future study should focus on how VOCs interact with different hormonal cascades during drought stress to fine-tune plant

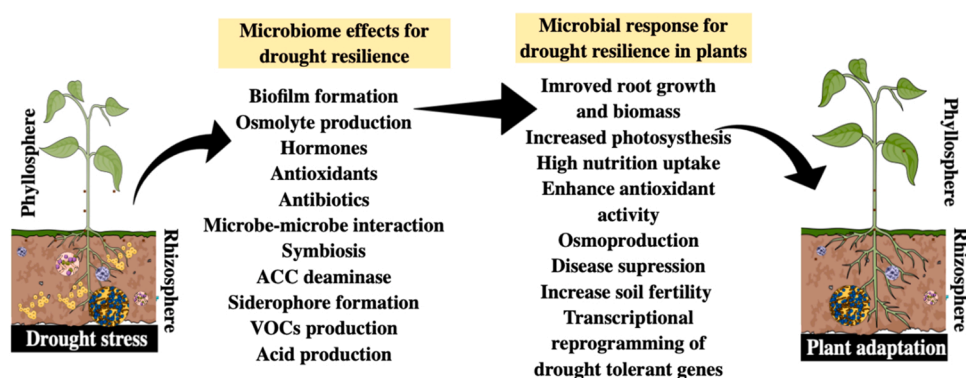stress resistance, expanding our knowledge of VOCs regulating signaling in plants during drought stress.

4.3. Microbes mitigate drought stress by inducing stress responsive genes

Microbial communities can aid plants in drought resistance by triggering transcriptional reprogramming of various genes and transcription factors involved in a variety of plant defense systems. For instance, Gowtham et al. (2021) reported that microbes can synthesize ABA or ABA analogs and trigger the induction of ABA related genes like, *ABA2, ABA3* and *NCED3* which are crucial for ABA production under stressful conditions. Another study have shown that *Trichoderma* and *Pseudomonas* inoculation in rice plants improve stress tolerance by increasing the transcript levels of numerous genes associated with phenylpropanoid biosynthesis pathway and the antioxidant enzymes (Singh et al., 2020). Other genes upregulated during drought stress include *DREB, DHN* (dehydrin), and *PiP* (plasma membrane intrinsic protein). Recent study have shown that *B. subtilis* strain GOT9 improves drought resistance in *Brassica campestris* and *A. thaliana* by inducing numerous drought tolerant genes *DREB1D, CSD3,* and *WRKY7* (*B. campestris*) and *NCED3, RAB18, RD20,* and *RD29B* (*A.thaliana*) (Woo et al., 2020). Abbasi et al. (2020) revealed that plant-associated microorganisms regulate *WRKY70* and *ERF1* in tomato plants, but promote antioxidant enzymes and proline accumulation. Govindasamy et al. (2020) revealed that root endophytic bacteria increase the transcript levels of pyrroline-5-carboxylate synthase genes such as *SbP5CS 1* and *SbP5CS 2* in maize under drought. Similarly, Saddique et al. (2018) reveled that rice seedlings treated with *P. indica* showed an upregulation of P5CS genes, which are important for proline biosynthesis, as well as increased phosphate and zinc uptake to ameliorate drought stress. Furthermore, soybean plants inoculated with *Pseudomonas simiae* improves growth and drought resilience by increasing the transcript levels various key genes such as (DREB/EREB), water transporters (PIP, TIP), and osmoprotectants (P5CS, GOLS) (Vaishnav and Choudhary, 2019). Similarly, in Arabidopsis, *P. polymyxa* CR1 treatment increased the expression of *RD29A* and *RD29B*, which are known to play vital roles in drought resistance (Liu et al., 2020). Similarly, pepper plants inoculated with *B. licheniformis* K11 increases drought resilience by activating number of stress responsive genes like HSPs, vacuolar ATPase (VA), pathogensis related proteins-10 and dehydrin-like protein (Lim and Kim, 2013). Application of metabolomic and proteomic studies revealed that, upon the inoculation of *P. indica* in barley under water stress, several key genes encoding transporters, signaling proteins, key metabolic enzymes, and proteins critical for oxidative stress are upregulated (Ghaffari et al., 2019). Interestingly, AMF associated with apple seedlings have been shown to increase the transcript levels of genes, such as *MdMAPK7–1, MdMAPK20–1, MdMAPK17,* and *MdMAPK16–2* which are important players of signal transduction during stress (Huang et al., 2020). Therefore, plant-associated microbes engage in triggering transcriptional reprogramming during drought stress and in providing tolerance

by increasing the expression levels of drought-tolerant genes. In conclusion, drought tolerance in plants is greatly alleviated by microbiomes because of their versatile roles in several physiological, biochemical, and molecular processes. Furthermore, we have shown microbiome-assisted modulations in plants during drought stress, such as improving water holding capacity, improving soil structure, assisting bacterial colonization, enhancing biofilm formation, stabilizing and activating signaling pathways, and adjusting metabolic networks in plants to alleviate drought stress conditions (Fig. 3).

5. Factors shaping plant microbiome

In natural environments, plants coexist with a diverse group of microorganisms, such as bacteria, oomycetes, fungi, archaea, and viruses, which interact in intricate ways. In a fast-paced, high-stress environment, these interactions determine plant nutrition availability, development, and fitness, establishing the basis for the Holobiont theory, which considers plants and plant-associated microorganisms as a single evolutionary unit rather than separate entities (Uroz et al., 2019). In addition, the plant microbiome, often known as the second genome, is critical for plant health. Microbes are abundant in every part of the plant and play important roles in plant development and reproduction. High-throughput microbial profiling of different parts of plants and rhizosphere soil has shown a highly diversified and dynamic microbiome. Plant microbiome assembly is dynamically influenced by multifaceted interactions between microbes, hosts, and other environmental factors (Fig. 4). For instance, various host-based features such as plant species, genotypes, age, canopy type, and plant-derived compounds can greatly influence the microbiome structure. The comparative microbial profiling of wheat, maize, and sorghum has showed distinct microbiome compositions among these plants (Bouffaud et al., 2014). Plants that are phylogenetically distant from each other have more variance in associated microbiome compositions; as a result, phylogeny influences microbiome structure (Bouffaud et al., 2014). Various genotypes of the same species have distinct microbiome compositions, implying that the microbiome is shaped by host genetics (Bodenhausen et al., 2013; Bulgarelli et al., 2015). Plants can also harbor distinct microbial communities in their parts like roots, shoots, leaves, flowers and fruits. Similarly, microbiome structure also varies with plant age. For example, in potato, maize, and soybean, plant age has a significant effect on the composition of the microbiome. Numerous factors like soil type and structure, daytime length, season, host features (developmental stage, species, parts) as well as exudates can dynamically influence or shape the microbiome (Vorholt, 2012). At the start of the growing season, soil and its properties (organic matter, depth, pH, porosity, oxygen, and carbon dioxide concentration) can have a great influence not only on subterranean microbial communities, but also on aboveground phytomicrobiomes (Copeland et al., 2015). The structure of the plant microbiome is determined by various intrinsic factors, like vertical transfer through seeds, plant organs, plant characteristics, and

Microbiome effects for drought resilience

Biofilm formation
Osmolyte production
Hormones
Antioxidants
Antibiotics
Microbe-microbe interaction
Symbiosis
ACC deaminase
Siderophore formation
VOCs production
Acid production

Microbial response for drought resilience in plants

Imroved root growth and biomass
Increased photosysthesis
High nutrition uptake
Enhance antioxidant activity
Osmoproduction
Disease supression
Increase soil fertility
Transcriptional reprogramming of drought tolerant genes

Phyllosphere
Rhizosphere
Drought stress

Phyllosphere
Rhizosphere
Plant adaptation

Fig. 3. Role of the plant microbiome in alleviating drought stress in plants. This process involves two steps: 1) Microbiome effects for drought resilience. Microbes undergo drastic transcriptional and metabolic reprogramming (as shown in figure) in order to survive under drought stress. Host exudates also play key role in activating microbiome factors for drought tolerance. 2) Microbial response improves drought resilience in plants by modulating various morphological, physiological, biochemical and molecular traits as shown in figure. In addition, during drought stress, microbes secrete diverse compounds that either directly or indirectly protect plants during drought stress.
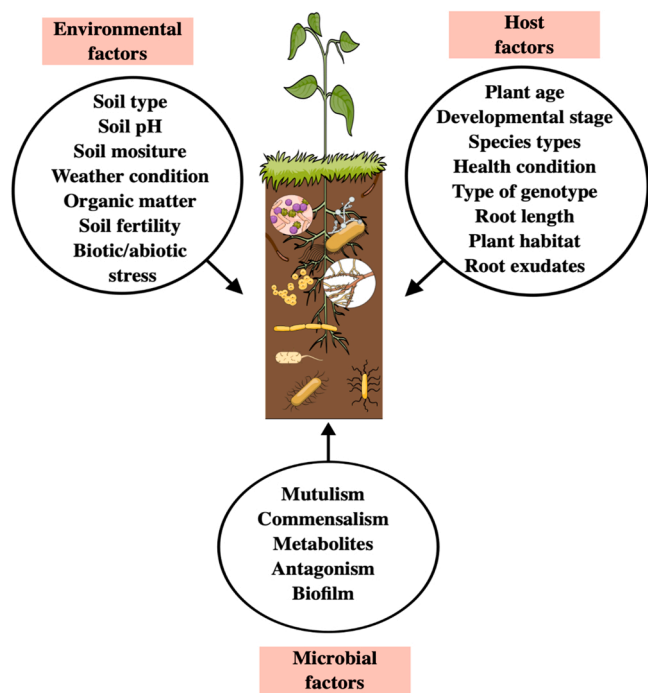
Fig. 4. Plant microbiomes are structured and form complex interconnected microbial networks that are directly influenced by the combined effect of plant, microbe, and environmental traits. Here, we schematically illustrate the factors influencing the plant microbiome structure and diversity.

plant-microbe interactions. Long-distance transport processes have a greater impact on the microbiota of aerial plant parts, whereas soil type, water and nutrient content have a greater impact on the microbiota of the roots (Bogino et al., 2013). Environmental factors such as radiation, wind, rain, pollution, and nitrogen fertilization, as well as age and shape variation among aerial parts of the plant, can influence different microbial community structures in the phyllosphere (Vorholt, 2012). The phyllosphere has a more dynamic environment than the endosphere and rhizosphere, which places great pressure on the phyllosphere microbiome assembly. While rhizosphere and soil microbial populations have some, there is little commonalities between open-air and phyllosphere microbial communities. Many factors like EPS, biofilm, adhesion molecules, flagellum, biosurfactant compounds, antibiotics, free radical detoxifying proteins, and quorum sensing signals play important roles in colonizing not only the phyllosphere microbiome but also the rhizosphere or endosphere microbiomes (Vorholt, 2012). Epiphytic bacteria produce pigments as a defense against ultraviolet light, which is necessary for their survival. Other features, including as stomata, trichomes, veins and hydathodes can have an impact on nutrient availability which can influence the phyllosphere microbiome distribution (Leveau and Lindow, 2001). Proteobacteria appeared to be the dominant colonizers in phyllosphere, followed by Bacteroidetes and Actinobacteria. Generally, microbial abundance is maximum in the soil, followed by rhizosphere and endophphere, indicating a significant selection gradient.

Plant exudates are important in microbiome selection and modifying exudation patterns to select a favorable microbiome may reveal new avenues for improving plant performance, with specific benefits for agricultural output. Exudates can contain amino acids, sugars, growth factors, vitamins, fatty acids, organic acids, and other chemoattractants that can influence the microbiome assembly in the phyllosphere and rhizosphere (Vives-Peris et al., 2020). Additionally, plant exudates like flavonoids, coumarins, camalexin, benzoxazinoids, malate, citrate, oxalate as well as ET, can selectively recruit microbial communities in the phyllosphere and rhizosphere. Plant immunity signature hormones, SA

and JA, and their signaling cascades greatly influence the microbiome structure in plants. For example, activation of JA pathway in plants, whether caused by exogenously or wounding results in an increased colonization of beneficial mycorrhizae in *Medicago truncatula* (Landgraf et al., 2012). Similarly, distinct phyllosphere and root endophyte microbial populations were detected in plants with altered SA signaling (Lebeis et al., 2015). Plant-associated microbiome can also secrete VOCs, which can alter the plant exudate composition in neighboring plants, which in turn influences microbiome assembly. Interestingly, the emitting and receiver plants display a large resemblance to their rhizosphere-associated microbial communities (Kong et al., 2021). Besides above factors, environmental cues like drought, salinity, heat and waterlogging can also influence the microbiome assembly in plants, which puts selective pressure on its members to survive under such conditions. For instance, the drought-induced glycerol-3-phosphate (G3P) synthesis in the plant roots favors Actinobacteria, which can efficiently uptake and utilizes G3P to sustain growth (Xu et al., 2018). In maize plants, drought-induced benzoxazinoid defenses in aboveground tissues and terpenoid phytoalexins in subterranean tissues may have an effect on phyllosphere and rhizosphere microbiome assembly (Vaughan et al., 2018). Drought reduces SA production, which have huge influence on the assembly of both external and internal microbiomes (Lebeis et al, 2015). Previous studies have shown that plants promotes gram positive bacteria or enrich monoderm over gram negative bacteria or diderm in the rhizopherere during drought stress (Naylor et al, 2017; Naylor and Coleman-Derr, 2018; Xu et al, 2018). Drought lowers the availability of phytosiderophore and iron in the rhizosphere, favoring Actinobacteria, which can flourish in iron-deficient environments, promoting plant development (Xu et al, 2021). These studies showed that drought has a negative impact on the plant microbiome, but some members can withstand drought by employing a variety of mechanisms to ensure their survival in the soil, assisting their host to cope with drought while increasing soil fertility.

6. Plants "cry for help" during drought stress and restructure their microbiomes to drive fitness benefits

The microbiome and host plant engage in subterranean and aboveground chemical communication to detect unfavorable conditions. For example, plants produce diverse metabolites during stress which recruit specific microbial communities capable of enhancing stress tolerance in plants (Liu et al, 2020). According to the developing "cry for help" assumption, plants recruit distinct microbial communities that help them cope with stress (Liu et al, 2020). This assumption was first time noted when plants recruit nitrogen-fixing rhizobia and nutrient-providing AM fungi grown under low nitrogen or phosphate levels (Carbonnel and Gutjahr, 2014; Nishida and Suzaki, 2018). Similarly, *Arabidopsis* recruit a special synergistic group of microbes after being infected with *Hyaloperonospora arabidopsidis* that helps to combat infection as well as and protects against future disease outbreaks (Berendsen et al., 2018). Recently, the subterranean "cry for help" perception was further supported by the results obtained from field experiments utilizing *Triticum turgidum* which was naturally infected by *Fusarium graminearum* and then enriched with *Stenotrophomonas rhizophila* (SR80) in the rhizosphere and root endosphere, which triggered ISR and enhanced growth (Liu et al., 2021). The "cry for help" hypothesis also applies to plants during drought stress. For example, the composition of the microbiome in roots undergoes significant alterations during drought, favoring Actinobacteria and other gram-positive bacterial communities over gram-negative taxa (Santos-Medellín et al., 2017; Timm et al., 2018). Similarly, plants can also recruit selective drought-resilient microbiomes, which may be an inherited trait, as a result of generations of repetitive droughts that have resulted in the evolution of steady and positive plant-microbe communications that advance both host and microbe reproductive fitness (Naylor and Coleman-Derr, 2018). Previous study has shown that *Brassica rapa*

plants exposed to drought stress drive increased and diversified bacterial richness around roots than control plants (TerHorst et al., 2014). Plants adapt to drought stress by reprogramming the chemistry of their root exudates to shape stress-resilient and health-promoting microbiomes. For instance, drought stress causes a plant-driven shift in the above-and belowground microbiomes, including an enrichment of drought-resistant endophytic monoderm bacteria that can aid in drought mitigation (Santos-Medellín et al., 2021). However, it was previously unknown how the period and intensity of drought affected the microbiome, as well as whether the microbes fully recovered after prolonged drought stress. Recently, Santos-Medellín et al. (2021) showed that long-standing drought can permanently delay the expansion of the plant endophytic microbiome, which persists even after the drought stress is relieved. This study showed that long-term abiotic stress can reconfigure a microbial community, which could have implications for plant health. This study also identified that drought-tolerant endophytic microbes that became more copious in the endosphere after drought stress may be potential candidates for microbiome engineering to develop elite microbial consortia to alleviate future drought stress in sustainable agriculture. Many studies have highlighted the significance of microbiome in drought resistance in various crops (Walters et al., 2018; Xu et al., 2018; Zhang et al., 2019). Active recruitment of beneficial microorganisms during stress conditions appears to be a common evolutionary strategy for improving plant fitness. However, the mechanisms that allow hosts to integrate external cues with the recruitment of beneficial microorganisms are still under investigation. These processes are governed by complex traits, which involve plants, microbes, soil, and other environmental factors, that define the overall outcome.

In addition, the host genetic traits that are involved in shaping the protective microbiome during drought stress are poorly understood. We are still in the early stages of understanding subterranean chemical communication, especially in drought-stressed plants that shape their resilient microbiomes. Drought-induced accumulation of stress response factors, such as pipecolic acid and glycerol-3-phosphate, in roots has been related to the enrichment of Actinobacteria in the rhizosphere (Naylor et al., 2017; Caddell et al., 2020). To unravel the complexities of the "cry for help" hypothesis in plant microbiome interactions before and after drought stress, a mechanistic understanding of the role of metabolic signatures and their genetic aspects is required. This will contribute novel insights into the development of drought-resistant microbial consortia for sustainable agriculture. In this review, we propose a model of the "cry for help" hypothesis in plants during drought stress from the plant microbiome perspective (Fig. 5). First, during drought, plants undergo metabolic and molecular reprogramming and secrete selective root exudates (primary and secondary metabolites). These root exudates can aid in restructuring or reshaping the microbiome by recruiting and selecting specific drought-resilient microbiota with diverse enzymatic activities. Finally, these drought-resilient microbial communities can have direct and indirect mechanisms that alleviate drought stress and provide nutrition among other benefits to the host plants.

7. Developing drought-resilient microbial communities: present understanding and knowledge gaps

The current challenge in fully exploiting the potential of the plant microbiome in sustainable agriculture is that its reliant on numerous factors, including the plant genotype, soil type, microbial interactions, management practices, and interactions among these factors (Busby et al., 2017; Soman et al., 2017; Schmidt et al., 2019). Hence, comprehensive systems biology approaches as well as the integration of multiomics are required to investigate the complexity of both host and microbial genetic and metabolic features that influence the phytomicrobiome. In recent years, the microbial world has received much attention owing to its low sequencing costs, which has allowed researchers to conduct in-depth investigations into their composition and to explore the complexities of host-microbiome interactions (Rodriguez et al., 2019). Metagenomics and metatranscriptomics have provided valuable information, not only for describing taxonomic changes in microbial taxa abundance but also in enabling researchers to unravel additional information regarding microbial functions. Additionally, proteomics and metabolomics have revealed the presence of functional proteins and metabolites in plant microbiome interactions. Because of the richness and complexity of plant-associated microbiomes, studies on metabolites produced in situ are limited due to the intricacy and heterogeneity of the their environment. In this review, we present examples highlighting the role of multiomics in deciphering how plant exudates shape plant microbiome during stress or natural conditions. For example, a combined amplicon-based metagenomic and metabolomic analysis of wild and benzoxazinoid precursor mutant maize genotypes revealed that benzoxazinoid metabolites contribute significantly to structuring the rhizosphere microbiome (Hu et al., 2018). Using joint shotgun metagenomics and metabolomics tools, Stringlis et al. (2018) determined that coumarin exudation from roots can influence the microbiome in *Arabidopsis* (wild and mutant) plants. A similar approach
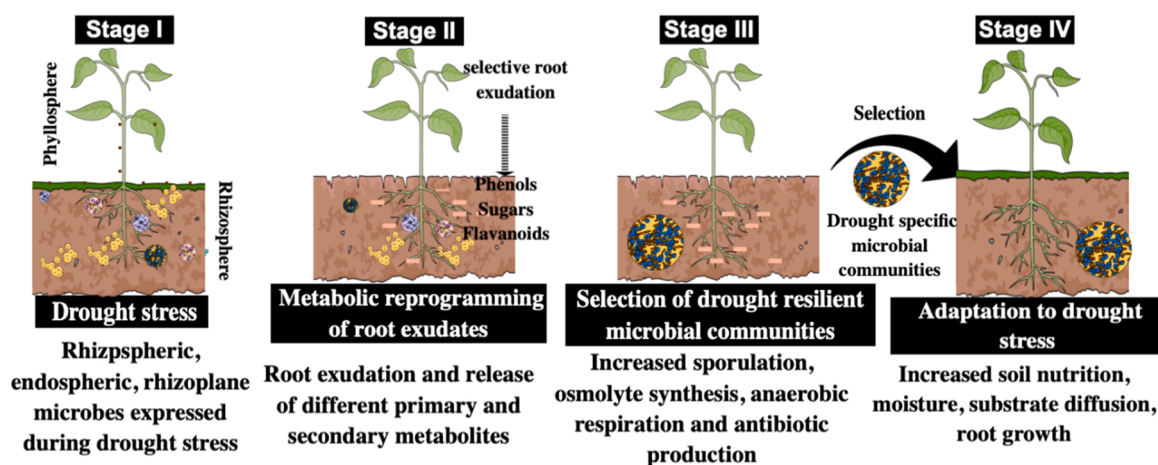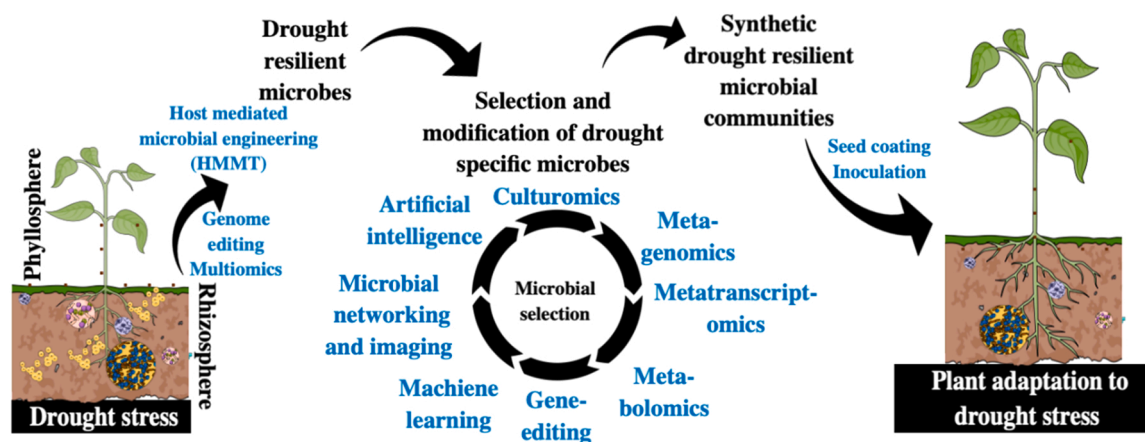

Fig. 5. Schematic representation of the "cry for help" hypothesis in plants during drought stress (from the plant microbiome perspective). In the first step, when plants face drought stress, they undergo metabolic and molecular reprogramming and secrete selective exudates (primary and secondary metabolites). These exudates can aid in restructuring the microbiome (above and below ground) by recruiting and selecting specific drought-resilient microbiota with diverse enzymatic activities. Finally, these drought-resilient microbial communities can have direct and indirect mechanisms that not only alleviate drought stress but also provide nutrition and other benefits to host plants.

was used in a previous study to investigate how triterpenes (root exudates) influence the compostion of the root microbiome in Arabidopsis (Huang et al., 2019). Furthermore, a multiomics study have revealed that the influence of root exudates at different developmental stages shapes particular microbial communities with distinct functional traits (Zhalnina et al., 2018). Hence, multiomic approaches, along with synthetic biology, may be useful in identifying drought-resilient microbes of the plant microbiome (Fig. 6). Current drought resistant microbial inoculants are typically comprised of a individual strain which are selected based on their PGP properties. Despite their widespread use, these approaches fall short of capturing important aspects of plant-microbe interactions, and researchers have switched their attention to more effective alternatives. Interestingly, plant microbiome comprises dynamically diversified microbes that drive many beneficial multifaceted traits in plants such as improving growth and yield as well as stress resilience (Compant et al., 2019). Nonetheless, there may be selective members in the plant microbiome that are driving beneficial functions to plants; thus, identifying these strains can be valuable for their future use in sustainable agriculture. The features favorable to the plant are the result of the synergistic and collective outcomes of these few critical members, which can be used to develop more robust methods that can overcome the constraints of traditional bioinoculants. Engineered microbiomes are more productive than traditional bioinoculants because they possess several plant-beneficial features, are resistant to being outcompeted, and respond swiftly to stimuli due to the division of labor (Alnahhas et al., 2020; Karkaria et al., 2021). The recognition of microbiome engineering's potential for improving plant health during stress has prompted research in this area. Further, this field has grown in popularity because of the advantages it has over single inoculation based methods. In this regard, harnessing plant microbiomes and their cocktails during drought stress in both wild and crop plants could provide novel avenues for developing elite drought-resilient SynComs for sustainable agriculture. Two key microbiome engineering techniques for drought stress management include the development of SynComs and HMME. SynComs comprises a relatively recent strategy that entails building inoculants based on notions from microbial ecology and genetics, as well as functions that promote plant characteristics, efficacy, and plant-microbe and microbe-microbe interactions (Arif et al., 2020). However, there are few reports on the development and testing of SynComs in a variety of hosts to improve drought resilience and enhance plant growth. For instance, Rolli et al. (2015) developed SynComs using Bacillus, Acinetobacter, Sphingobacterium, Delftia, and Enterobacter in grapevines, which confer not only to drought tolerance but also improve growth features. Similarly, SynComs containing Sphingomonas, *Pseudomonas putida*, and the Acinetobacter *Azospirillum brasilense* were developed, which confer not only drought tolerance in maize plants but also enhances plant height and shoot and root dry weight (Molina-Romero et al., 2017). These studies emphasize the significance of SynComs for drought resilience, and call for additional future research to uncover a robust drought-tolerant core microbiome that may be leveraged to produce elite SynComs for future drought-resistant smart crops. Many outstanding reviews have shown how to design SynComs with success and limitations (Ali et al., 2022). With the advent of synthetic biology, we are able to create tailored drought-resilient SynComs by adding or removing particular microbial members, which will enable us to investigate the roles of individual microbial members and the factors that shape their assembly. For example, the elimination of a *Enterobacter cloacae* strain from maize alters microbes capable of protecting maize from blight disease (Niu et al., 2017). In addition, computational methods, artificial intelligence, and machine learning will improve the practice of determining the finest amalgamation of microbes for a desired host phenotype by leveraging approaches for screening and identifying beneficial microbes (de Souza et al., 2020).

Microbiome engineering with precise and durable beneficial effects on crops poses a challenge to plant microbiome research. These difficulties in microbiome engineering are caused by several interconnected factors, including the complexity of microbiome communities and changes in microbiome function during plant ontogeny. In this regard, host-mediated microbiome engineering (HMME) provides an innovative tool for engineering long-term beneficial microbiome functions that makes use of the host phenotype to select microbiomes in an indirect manner through cyclic differentiation and propagation to maintain microbial communities that benefit plants. The key benefit of this method over SynCom production is that the desired microbes have already been chosen by the host and have become acclimated to stress situations. SynComs, on the other hand, exclusively utilize culturable bacteria, whereas the host-mediated strategy uses both culturable and unculturable microbes. To date, only a few experimental studies of plants have used this approach. Recently, Mueller et al. (2021) used the HMME strategy to identify the desired microbiome that can protect *Brachypodium distachyon* from salt stress. The selected microbiome increased seed production by (55–205%) compared to plants with unselected control microbiomes, in addition to improving salt tolerance. HMME can indirectly select microbiomes to improve growth traits during altered soil

Fig. 6. Schematic representation of the development of drought-resilient microbial communities in sustainable agriculture. Two strategies are undertaken here, namely, host mediated microbial engineering (HMME) and microbiome engineering (SynComs) for developing drought-resilient microbial communities in sustainable agriculture. HMME makes use of the host phenotype to select microbiomes in an indirect manner through cyclic differentiation and propagation to maintain only those microbiomes with the desired fitness effects of the host. SynComs can be developed by bottom up and top down approaches. Further, we also highlighted the role of multiomics, artificial intelligence, and machine learning in validating the role of engineered microbiomes or their traits during drought stress. This figure also highlights the application of perspective seed coating as a promising method to utilize drought-resilient microbial communities in sustainable agriculture.

pH conditions in *A. thaliana* (Swenson et al., 2000). Similarly, HMME has also been employed to harbor microbiomes capable of changing leaf biomass and flowering time (Panke-Buisse et al., 2015, 2017). On the other hand, Jochum et al. (2019) used HMME to enhance the drought resilience of wheat plants. Using 16 S rRNA amplicon sequencing of the selected microbiome, they discovered that Proteobacteria were abundant at the phylum level (Jochum et al., 2019). On the other hand, HMME was also used in mustard plants for improving drought tolerance (Lau and Lennon, 2012). Similarly, TerHorst et al. (2014) also used HMME approach to enhance drought resilience in mustard plants. According to the present study, both evolutionary and ecological responses are evenly important in influencing plant adaptation to stressors. The promising findings of above studies highlight the role of microbiome engineering in sustainably promoting plant development and reducing stress. In addition, we summarized the use of SynComs and HMME to improve drought resilience in various crops in Table 2. We also emphasize the importance of manipulating plant traits through genome editing to promote the desired drought-resilient core microbiome as an alternative to the traditional microbial applications for drought resilience. For example, Song et al. (2021) screened *Arabidopsis thaliana* mutants and discovered that the FERONIA a plant cell wall receptor like kinase mutant (fer-8) promotes *P. fluorescens* enrichment in the rhizosphere, concluding that FER inhibits Pseudomonas in the rhizosphere microbiome by regulating ROS. Many other essential plant features, such as hormonal pathways and genes coding for various plant exudates that are involved in shaping distinct microbiomes must be targeted during drought stress in order to determine their function in shaping drought-resilient microbiomes. Furthermore, we have shown how to develop and functionally validate a drought-resilient engineered microbiome for sustainable agriculture (Fig. 6).

8. Plant microbiome from lab to field: future perspective

Drought stress is becoming more frequent and lasting as a result of global climate change, reducing crop yield and quality. The plant microbiome has the potential to protect plants from drought stress while also increasing crop productivity and soil fertility. Plants dynamically recruit highly diversified microbes that provide vast benefits to them, and the associated microbiota are considered an accessory plant genome. The global population is rapidly increasing, necessitating an increase in food production. In addition to drought stress, climate change and soil pollution present challenging growing conditions for sustainable crops. In this regard, the plant microbiome may be able to address all problems that our current agricultural system is experiencing.

Owing to their beneficial traits, the plant microbiome and its cocktails form the focus of new product development in sustainable agriculture for future food security (Sessitsch et al., 2019). However, the present application of plant microbiomes under field conditions faces a number of confronts, and we suggest that a number of factors must be considered such as unraveling the intricacies and ecological behaviors of natural microbiome. Usually, microbes are screened for their beneficial traits under laboratory and controlled conditions, followed by greenhouse experiments using model plants. There has been enormous success under these conditions, as can be seen in many publications on plant-microbe interactions. However, when used in the field, these effects are highly variable and inconsistent, limiting the applicability of the microbiota. To be successful in using plant microbiome consortia under field conditions, the following steps must be taken: The first is an effective microbial consortium delivery system (with appropriate formulation) which protects microbes from dehydration and other undesirable environmental conditions. In this regard, introducing plant microbial consortia into the seed microbiome is an advanced tool for

Table 2
Application of microbiome engineering (SynComs/HMME) for mitigating drought stress in plants.

Synthetic microbial communities/consortia (SMC)				
SynComs	Plant species	Stress	Response	Reference
Strains of Acinetobacter, Bacillus, Sphingobacterium, Enterobacter and Delftia	*Vitis vinifera* cv. Barbera	Drought stress tolerance	Tolerance to drought stress by improved water holding capacity and reduction in water loss during desiccation. Root biomass increased two-fold compared to untreated plants	Rolli et al. (2015)
Strains of *Acinetobacter calcoaceticus, Burkholderia sp., Burkholderia vietnamiensis, Curtobacterium sp., Enterobacter asburiae, Pseudomonas sp., Rahnella sp., Rhizobium tropici, Rhodotorula graminis, Sphingomonas yanoikuyae*	*Populus deltoides X P. nigra* clone	Drought stress tolerance	Drought stress tolerance and plant growth-promoting activity enhanced root and shoot biomass, and total plant nitrogen compared to control plants	Khan et al. (2016)
Strains of *Pseudomonas putida, Sphingomonas, Azospirillum brasilense, and Acinetobacter*	*Zea mays*	Drought stress tolerance	Drought stress tolerance with enhanced plant height compared to mono-inoculated and uninoculated plants	Molina-Romero et al. (2017)
Strains of *Asticcacaulis, Bosea, Burkholderia, Dyella, Chitinophaga, Ensifer, Enterobacter, Lysobacter, Microbacterium, Pantoea, Pedobacter, Pseudoxanthomonas, Rhizobium, Sphingomonas, Stenotrophomonas,* and 2 unidentified genera of Comamonadaceae and Streptomycetaceae	*Zea mays*	Drought stress tolerance	Plant growth promoting activity with an increase in biomass by 3.4 fold, dark green leaves and increased branched roots in inoculated plants as compared to uninoculated plants	Armanhi et al. (2018)
HMME				
Microbes associated with wet environmental conditions increased	*Brassica rapa*	Drought stress tolerance	Plant growth parameters like fruit number, flower number, and days to flowering were monitored. Fruit and flower production increased when plants were raised with an adapted microbiome	Lau and Lennon (2012)
	Brassica rapa	Drought stress tolerance	The bacterial abundance and richness increased during adaptation. In the case of the fungal community, the richness increased but abundance decreased. There was an increase in soil nitrogen concentration and a reduction in carbon to nitrogen ratio during adaptation	TerHorst et al., 2014
Accumulation of Proteobacteria phyla increased while Actinobacteria and Acidobacteria decreased	*Triticum aestivum*	Drought stress tolerance	Symptom of delayed onset of water-deficit stress was recorded. Shifts in bacterial phyla were observed such as an increase in Proteobacteria phylum by 1.2-fold, whereas the relative abundance of Actinobacteria and Acidobacteria decreased	Jochum et al. (2019)

protecting microbes from environmental abrasions. In this method, microbial formulations are sprayed onto the flower parts of plants, where they colonize and integrate into the progeny seed. This will protect the introduced microbial strains from strong competitive pressure in the rhizosphere and soil habitats, similar to the natural seed microbiota, allowing them to colonize future plant generations at early growth stages. future plant generations at early growth stages. In addition, the use of plant beneficial endophytes has advantages owing to their ability to colonize plant tissues internally, with less community completion and develop long-term relationships with hosts. The second challenge is the development of metabolically and physiologically stable microbial consortia that can adapt to environmental fluctuations and efficiently colonize plants. Generally, microbes grown under laboratory conditions are grown under nutrient-rich, optimized growth conditions. Hence, nutritional, physiological and growth conditions may directly influence overall successful establishment and their competitive capability with other microbes in the field. Additionally, microbes are known to display either synergistic or antagonistic interactions with each other owing to their ability to secrete numerous antimicrobial compounds, as well as through other means such as quorum sensing, that may compete with other beneficial microbes (Sessitsch et al., 2019). Finally, there are potential concerns and hurdles that must be overcome prior to the regulatory approval of introduced microbial consortia to the environment. Because microbes cause a variety of plant diseases as well as food toxicity, there is widespread concern that their use could jeopardize not only plant health but also food safety. Thus, it is critical to ensure that the introduced microbes do not degrade the environment or endanger plants, humans or animals. In summary, the successful application of plant microbiomes for drought resilience in agricultural crops under field conditions first requires a number of factors to be implemented, including appropriate formulation design, increased shelf life, resistance to environmental cues, and a mechanistic understanding of their complexity and ecological behavior. Finally, continuous data transmission on the plant microbiome in the field could open up new avenues for plant microbiome applications and their performance in agriculture in addition bridging the gap between lab findings and field performance (Busby et al., 2017).

9. Conclusions and future directions

Plant breeders and crop physiologists face difficulties in improving drought resistance in agricultural plants because it is a complicated genetic trait involving several mechanisms. As discussed above, harnessing the potential of the plant microbiome and the development of elite drought-resilient microbial consortia via microbiome engineering may sustainably reduce the impact of drought in agriculture in the future. Plants have complex relationships with diverse microbes that boost their tolerance to changing environmental conditions. Although we have a good understanding of some of these alliances, we lack an in-depth understanding of the many other processes and alliances that plants form to withstand environmental stress. There are still many unanswered questions regarding how drought stress affects microbe-microbe interactions, plant-microbe interactions, and how they compete for survival. Understanding the full scope of plant-microbe interactions and how they change over time under drought conditions will open many new avenues for research concerning the improvement of plant resilience to drought stress. Future studies are required to unravel how drought stress induces physiological changes in plants that directly modulate the microbiome assembly in the phyllosphere, endosphere, and rhizosphere regions and how this modulation ultimately results in fostering microbiomes that aid plants in avoiding and/or tolerating drought stress. Additionally, engineered microbiomes are more productive than traditional bioinoculants because they possess several plant-beneficial features, are resistant to being outcompeted, and respond swiftly due to the division of labor. Although engineering microbiomes is becoming more popular owing to its benefits over

microbe-based engineering, there are numerous gaps in current knowledgebase that must be addressed to fully realize the associated beneficial outcomes. Such gaps include the (1) limitations of core microbiome identification, (2) lack of strategies for cultivating previously uncultivable microbial communities, and (3) variations among field and lab results. We also emphasize the importance of manipulating plant traits by genome editing to promote specific beneficial microbial members in the plant microbiome that will improve drought resilience. For example, cell wall receptors, such as receptor-like kinases, hormonal pathways, and genes coding for different plant exudates, are important targets for investigating their role in shaping the desired microbiome under drought stress. Finally, under drought conditions, plant promotion of specific microbial taxa may help to identify drought resilient microbial communities that promote not only growth but also stress resilience, which will help in the future to develop them into elite microbial consortia using synthetic biology to alleviate drought stress in sustainable agriculture.

CRediT authorship contribution statement

Hanhong Bae: Conceptualization, Investigation, Data curation, Project administration, Funding acquisition, Editing, Supervision. **Sajad Ali**: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Anshika Tyagi**: Conceptualization, Writing – original draft, Methodology, Formal analysis, Investigation, Data curation, Visualization, Editing. **Suvin Park**: Writing – original draft, Data curation. **Rakeeb A Mir:** Writing – original draft, Data curation, Editing. **Muntazir Mushtaq:** Writing – original draft, Data curation. **Basharat Bhat:** Writing – original draft. **Henda Mahmoudi:** Writing – original draft, Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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