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Understanding the plant-microbe interactions in environments exposed to abiotic stresses: An overview

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ABSTRACT

Abiotic stress poses a severe danger to agriculture since it negatively impacts cellular homeostasis and eventually stunts plant growth and development. Abiotic stressors like drought and excessive heat are expected to occur more frequently in the future due to climate change, which would reduce the yields of important crops like maize, wheat, and rice which may jeopardize the food security of human populations. The plant microbiomes are a varied and taxonomically organized microbial community that is connected to plants. By supplying nutrients and water to plants, and regulating their physiology and metabolism, plant microbiota frequently helps plants develop and tolerate abiotic stresses, which can boost crop yield under abiotic stresses. In this present study, with emphasis on temperature, salt, and drought stress, we describe current findings on how abiotic stresses impact the plants, microbiomes, microbe-microbe interactions, and plant-microbe interactions as the way microorganisms affect the metabolism and physiology of the plant. We also explore crucial measures that must be taken in applying plant microbiomes in agriculture practices faced with abiotic stresses.

1. Introduction

Different abiotic stressors influence and affect plant physiology. Abiotic stress causes several physiological changes in plants that may be adaptive reactions to the environment. These changes may be in the root, germination rate, growth, developmental transition and shoot architecture. The reduction in agricultural yields brought on by these physiological changes in plants, including their adaptive responses, has a profound impact on food security. Drought, extreme hot or cold temperatures, and the stressing chemical and physical characteristics of the soil are examples of such abiotic stressors (Osman, 2018; Kannojia et al., 2019; Jansson and Hofmockel, 2020; Zhang et al., 2022). The plant microbiomes are a varied and taxonomically organized community of microorganisms that includes viruses, fungi, archaea and bacteria that coexists with plants in natural and agricultural fields (Compant et al., 2019; Trivedi et al., 2020; Chialva et al., 2022; Fadiji and Babalola, 2020b). Plant-associated microbes can come from rain, soil, seed, the air, and other nearby living things like insects and animals. The term "holobiont" might best illustrate a picture of the plant and its associated microbiome, which can inhabit the endo- and ectosphere, and whose interactions can be influenced by the environmental factors (Vandenkoornhuyse et al., 2015; Trivedi et al., 2020).

Plant-associated microorganisms frequently support plant health and growth by making use of different plant growth promoting (PGP) mechanisms, including improvement of mineral solubility (Lemanceau et al., 2017); altering the signaling of phytohormones including auxin, cytokinin and gibberellin (Joo et al., 2005; Spaepen and Vanderleyden, 2011); and directly supplying nutrients (Garcia De Salamone et al., 1996), alongside enhancing the resistance to phytopathogens (Bakker et al., 2013). Plant-associated microorganisms have garnered interest from researchers for use in agriculture because they influence plant physiological parameters under abiotic stress conditions and encourage plant development and tolerance to abiotic stresses (Vejan et al., 2016; Ma, 2019; Bhat et al., 2020; Hou et al., 2021a; Fadiji et al., 2022a).

Abiotic stress alters not only the plant's physiology and metabolism but also the soil microorganisms. Additionally, the impact of abiotic stresses on one thing (like a plant) impacts other things (such as microbes). As a result, there is a close connection between soil, plants,

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abiotic stress and the associated microorganism. Additionally, the results of stress vary depending on circumstances including the time of experiencing stress, the species of the host plant, the intensity of the stress, and similar variables of the environment. Thus, under abiotic stress conditions, associations between the microbes and plant are dynamic and complicated.

Subsequently, crop plants are frequently subjected to a variety of environmental stressors, such as drought, acidity and salinity of the soil, UV radiation, intense light, temperature, nutritional shortages, and toxicity, which have a significant negative impact on crop output globally. According to the Food and Agriculture Organization's 2016 study, the agricultural production must rise by nearly 60% by 2050 in order to feed the growing world population (FAO, 2016). The yields of the main cereal crops will also decrease by 20–45% for maize, 5–50% for wheat, and 20–30% for rice by the year 2100 because of the global climate change in addition to other abiotic stresses (Inbaraj, 2021). Abiotic stressors' direct and indirect effects are having a negative influence on agricultural productivity at an exponential rate. Global food security is now seriously threatened by the significant climate changes occurring around the world as well as the tremendous growth in population globally (Lesk et al., 2016). To fulfill the demands of a growing population, it is necessary to increase the resistance of crops to diverse abiotic stressors and assure high agricultural output in difficult conditions (Pereira, 2016).

To use plant microbiota for agriculture, it is essential to comprehend how abiotic stressors affect plants, microbe-microbe interactions, microorganisms, soil-microbe interactions, and plant-microbe interactions. In this paper, we discuss and summarize the current development in plant-microbiome interactions in plants faced with abiotic stresses, with a special concentration on temperature, salt, flood, and drought stresses, which are known to significantly harm the production of the crop (Osman, 2018; Gupta et al., 2020; Sarkar et al., 2022; Fadiji et al., 2022b). Although abiotic pressures also influence how pathogens and plants interact, this will not be explored in this current study but will point readers to recent, good reviews on the subject (Velásquez et al., 2018; Cheng et al., 2019; Saijo and Loo, 2020; Zarattini et al., 2021). Fig. 1 illustrates a general view of diverse abiotic stressors on plant growth and development, taking wheat crop as an example. The figure is adapted from Khadka et al. (2020), who highlight the effect of drought on the development of wheat plants. However, other types of stress related to drought, such as high temperatures, UV rays, fire, among others, can have similar negative effects on wheat crops during their

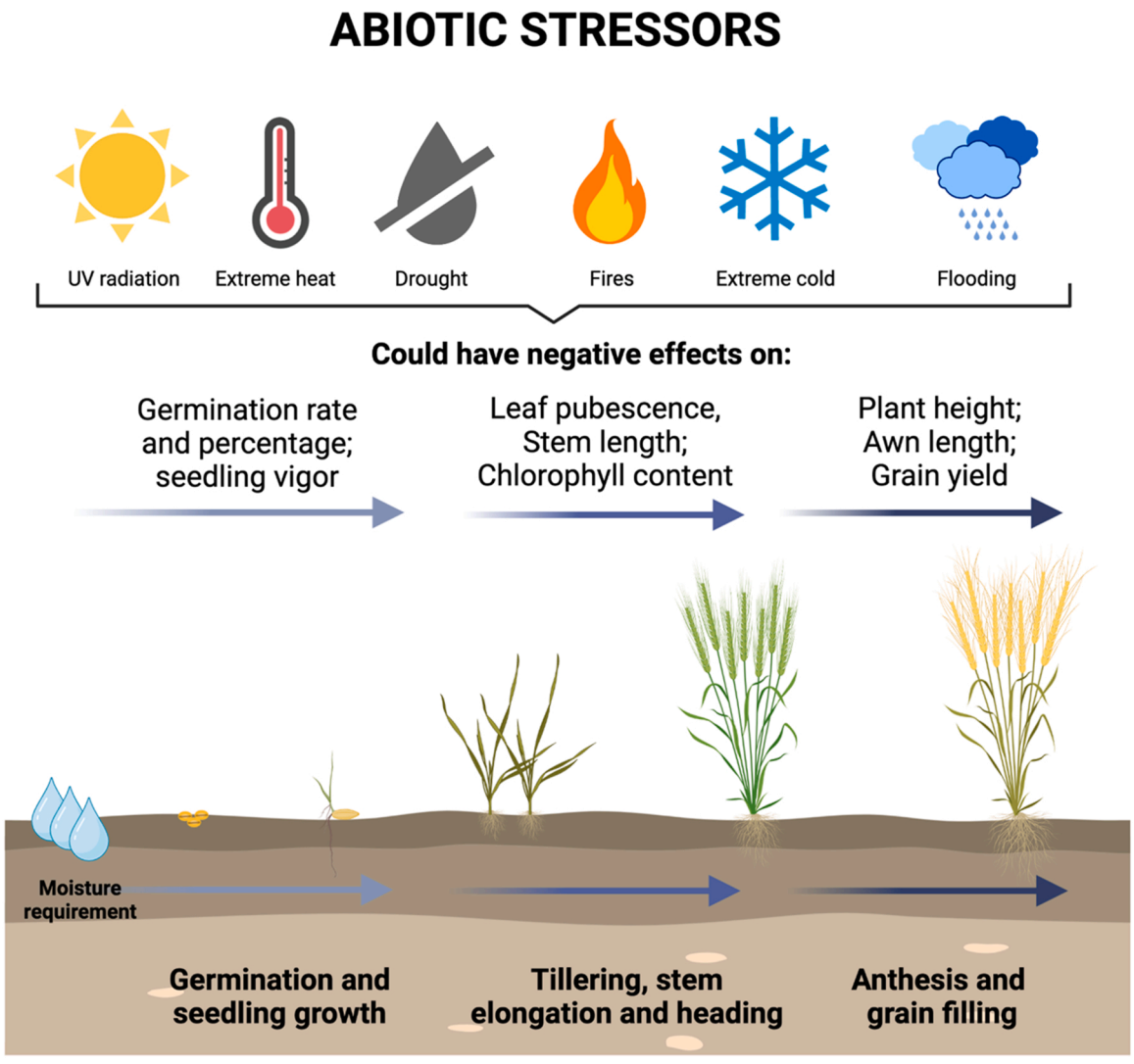

Fig. 1. Impact of abiotic stressors on different stages of the plant growth and development. Stresses could hava negative impact on germination rate and percentage, as well as seed vigor in the fisrt stages of germination and seedling growth. Then, tillering, stem elongation and heading stages could be stressed and lead to a lower chlorophyll content, a reduction in leaf pubescence and stem length. Finally, stressor may impact on the plant height, awn length and reduce grain yield in the last stages of the plant (anthesis and gran filling).

different stages of their growth. In this same work, the authors mention that wheat-producing areas of the world are those manly prone to suffer in the next years by drought.

2. Combined effects of abiotic stresses on plants

The physical environment that plants live in is always changing in many ways. The basic building blocks for plant development are water, mineral nutrients, energy (light) and carbon (Cramer et al., 2011). Drought, salinity, radiation, extreme cold and heat, floods, nutritional deficiencies, and heavy metals all have a detrimental effect on plant development and growth (Kul et al., 2020). Examples of abiotic factors that have an impact on a plant's performance include a severe temperature, lack of water, soil nutrients, soil salinity hardness and excess light (Yadav et al., 2020). A combination of salinity and drought stresses affects almost 50% of the world's farmed fields (Abdelraheem et al., 2019). Because of this, understanding the responses of agricultural plants to abiotic stress has drawn the attention of plant scientists. Abiotic stresses have both reversible and irreversible effects on how plants react (Javed et al., 2022). Biochemical, physiological, molecular, and cellular studies of plant abiotic reactions have shown complex biological responses to abiotic stresses. Furthermore, the intricacy of the reaction can be significantly influenced by the length and degree of the stress, whether it is chronic or acute (Javaid et al., 2022). The biochemical, physiological, and morphological processes that are directly connected to crop production and associated qualities are negatively impacted by abiotic stressors (Yadav et al., 2020).

Plants are negatively impacted by drought stress at all phases of development and growth, from the morphological to the molecular levels (Islam et al., 2016). By raising the osmotic pressure outside the roots, abiotic stressors like salt affect the roots of the plant (Yadav et al., 2020). Reduced water intake and accumulation into developing cells cause enzymatic changes in the cell wall that impede plant growth (Javed et al., 2022). Water shortage largely inhibits photosynthesis and respiration, which in turn limits plant development. All cellular processes were interrupted by cold stress, which also resulted in reduced electrolyte leakage, plasmolysis and protoplasmic streafiming, all of which adversely affected the cells in different ways (Yadav et al., 2020). In addition to osmotic stress, salinity also causes ionic toxicity, which is connected to the deficiency of nutrient and oxidative damage. Due to ionic toxicity and osmotic stress, plants cannot grow or develop at high salt concentrations (Singhal et al., 2022). Under salt stress circumstances, soil osmotic pressure surpassed plant cell membranes, preventing plants from absorbing nutrients like Ca^{2+} and K^{+} and harming their growth and cell membranes. Due to increased ion toxicity and osmotic potential, high soil salinity hinders plant development and growth stages in addition to preventing the germination of seed (Javed et al., 2020).

Furthermore, under the combined effects of abiotic stresses, several physiological systems, including respiration, photosynthesis, nitrogen fixation, and starch metabolism are impacted, which reduces agricultural productivity (Farooq et al., 2015). Physiological alterations include decreasing relative stress damage, rising nutritional imbalances, and decreasing water potential, relative water content and leaf osmotic potential. Leaf withering, leaf abscission, a reduction in leaf area, and a reduction in water transpiration are further stress physiological responses (Fghire et al., 2015). Turgor pressure, a crucial physiological process influencing cell development under drought stress also reduces (Yadav et al., 2020). Additionally, among other effects, the pressure of dryness results in elongated cells, compromised mitosis, and shorter plants (Ismail et al., 2021).

Plants produce protective compounds in response to drought by mobilizing metabolites to change their osmotic equilibrium (Gull et al., 2019). Through the preservation of cell water balance, osmotic adjustment can lessen the negative consequences of stress (Fghire et al., 2015). When cold stress causes cells and tissues to dry and crystallize, which results in electrolyte leakage, decreased membrane conductivity, and increased water viscosity, plant growth and development are inhibited (Bahar et al., 2021). Before it limits growth, water shortage reduces respiration and photosynthetic activity. The freshly split cells that surround the xylem restrict plant development zones due to their fundamental nature. Both high temperatures and stresses associated with irreversible drought that can cause plant death to influence the growth and development of plants (Hussain et al., 2019). During the reproductive development stage, heat stress often causes cells to stop functioning, which results in a dysplastic anther (Gull et al., 2019).

Additionally, several molecular pathways engage in crosstalk and interactions as the plant responds to abiotic stressors. ROS and Reactive nitrogen species (RNS) are key players in a variety of abiotic stress responses, influencing gene expression and enzyme function (Mittler et al., 2011). Cells engage a number of reactions in response to ROS, including boosting the expression of genes involved in antioxidant activities, generating stress proteins, activating antioxidant enzymes, and assembling suitable materials (Sardhara and Mehta, 2018). Abiotic stress can also be decreased by the presence of certain detoxifying genes such glutathione peroxidase, glutathione reductase and ascorbate peroxidase. Hormones (such as abscisic acid and ethylene) can also control abiotic stress responses in plants (Goda et al., 2008). Abscisic acid (ABA) is crucial in many plants for controlling osmotic stress. Slower responses to ABA include systems for growth, germination, and protection. There are several mechanisms by which cold stress signals are sent, including ROS components, protein kinase, protein phosphate, ABA, and Ca^{2+}, although ABA seems to be the most efficient one (Gull et al., 2019). In response to water stress during seed dehydration, late embryogenesis abundant proteins (LEA) accumulate in enormous numbers during early embryogenesis (Gull et al., 2019). In addition to drought and ozone, ethylene also has a role in cold, UV radiation exposure, cold and floods (anoxia and hypoxia) (Yoo et al., 2009).

3. Drought stress

3.1. Impact of drought stress on the assembly of microbial communities

The structure of the microbial population in the endosphere and rhizosphere of the root and root is impacted by drought (Furze et al., 2017). Naylor et al. (2017) looked at how drought affected the community structure of bacteria in roots, bulk and rhizosphere soils of different hosts that are of grass origin. The result showed that drought resulted in a decline in the variety of organisms from the soil to the roots and an enrichment in the Actinobacteria abundance across all species, which was mostly due to the presence of genus *Streptomyces* (Naylor et al., 2017).

A recent work published by Canarini et al. (2021) mention about the formation of "ecological memory" in the soil that is subject to recurrent droughts and that can improve the resilience of the functioning of ecosystems in the face of future droughts thanks to the role played by the microorganisms that inhabit these ecosystems. Such conclusions are derived from a work where a long-term field experiment was carried out in a mountain grassland (located in central Austria) with an experimental layout comparing 10 years of recurrent drought events and comparing it with a single drought event. Likewise, it was interesting to note that soil multifunctionality is measured as potential enzymatic activities, microbial biomass stoichiometry, soil nutrients, and belowground net primary productivity. This was stimulated by recurrent droughts as compared to single drought events. Therefore, the ecological memory should be explored in different soil agroecosystems subjected to other similar stresses, including fire, and heat stress. Perhaps in a near future some of these resilient microorganisms can be key agents to improve plant growth and health under harsh conditions.

3.1.1. Assembly of bacterial community

The rhizosphere and endosphere of the root microbial community

structure are impacted by drought (Sun et al., 2017; Furze et al., 2017). Fig. 2 provides an overview of how drought affects interactions between microbes and the plant. The impacts of drought on the structure of the community of bacteria in the bulk soil, rhizosphere and the roots of eighteen grass plants were examined by Naylor et al. (2017). Except for the genus Streptomyces, drought decreased alpha diversity from roots down to the soil and increased the abundance of Actinobacteria in most species identified (Naylor et al., 2017). It is important to determine whether the declining abundance of other taxa of bacteria was the cause of their declining relative abundance.

Interestingly, the bacterial community's resemblance to the host's phylogenetic distance was most pronounced in the roots (Naylor et al., 2017). Although dehydration caused significant changes in the bacterial community composition that caused this congruency to decrease in younger plants, it was preserved in older plants, indicating the introduction of a more excellent selection of hosts in the community structure of bacteria later in the growth of the plant (Naylor et al., 2017). According to the research, the early community of bacteria is drought susceptible compared to the late bacterial community because the effects of drought on the bacterial population of the root were greater at a younger developing stage than at an older development phase (Xu et al., 2018).

Similar results were found in different studies which examined the endosphere microbiome of the root of thirty angiosperm species under drought stress and found an enrichment of Actinobacteria taxa like the abundance of the genus *Streptomyces* (Fitzpatrick et al., 2018). Across many research (Dai et al., 2019; Simmons et al., 2020), relative abundances of Actinobacteria often rise, whereas Proteobacteria and Bacteroidetes tend to decrease under drought stress. According to studies on rice and millet, the dominance of Actinobacteria level during drought stress was consistently connected with the severity of drought (Simmons et al., 2020; Santos-Medellın et al., 2021). As a result, drought-induced enrichment of taxa of Actinobacteria like *Streptomyces* in the underground sections of plants was highly preserved among ecologically varied plant species. The community composition of bacteria was dependent on the stage of plant growth, and the root endosphere had a higher Streptomyces spp. enrichment level than the rhizosphere and bulk soil (Naylor et al., 2017; Fitzpatrick et al., 2018; Xu et al., 2018). These findings suggest that either *Streptomyces* spp. are recruited by the plants and have some useful functions for plants, or that *Streptomyces* has unique adaptations for dry conditions near roots. The capacity of actinobacteria to withstand drought conditions, including the formation of spores and strong cell walls, was thought to be the cause of the enrichment of actinobacteria (Tocheva et al., 2016). It is worthy to note, however, that metatranscriptome research showed that drought enhances the transcription of particular Actinobacteria genes, particularly those who are involved in roles such as metabolite transport, carbohydrates and amino acids. This shows that the Actinobacteria enrichment in drought stress is related to both their active adaptation to the dry conditions as well as their high endurance of dehydration, which are peculiar to Actinobacteria spores (Xu et al., 2018).

Due to the uneven distribution of soil moisture, various plant roots may experience dryness in different ways. Local or systemic changes in the microbial populations of the roots, such as the Actinobacteria enrichment, might take place. Actinobacteria enrichment was seen in a single millet, but not in roots that were receiving adequate water. This indicates that the localized region of drought stress is where Actinobacteria enrichment occurs (Simmons et al., 2020). Additionally, under drought, Actinobacteria enrichment was not observed in roots that are dead (Simmons et al., 2020). According to these findings, plants actively control Actinobacteria enrichment. Although a method has recently been described, our knowledge of the way plants controls the conserved Actinobacteria enrichment taxa like Streptomyces under drought is still restricted (Xu et al., 2021).

Time-series transcriptome analysis of the root of the sorghum plant revealed that drought had an impact on the host's metabolism of iron, resulting in decreased iron uptake activity and an increment in iron storage. Sorghum TOM1 homolog expression was also significantly

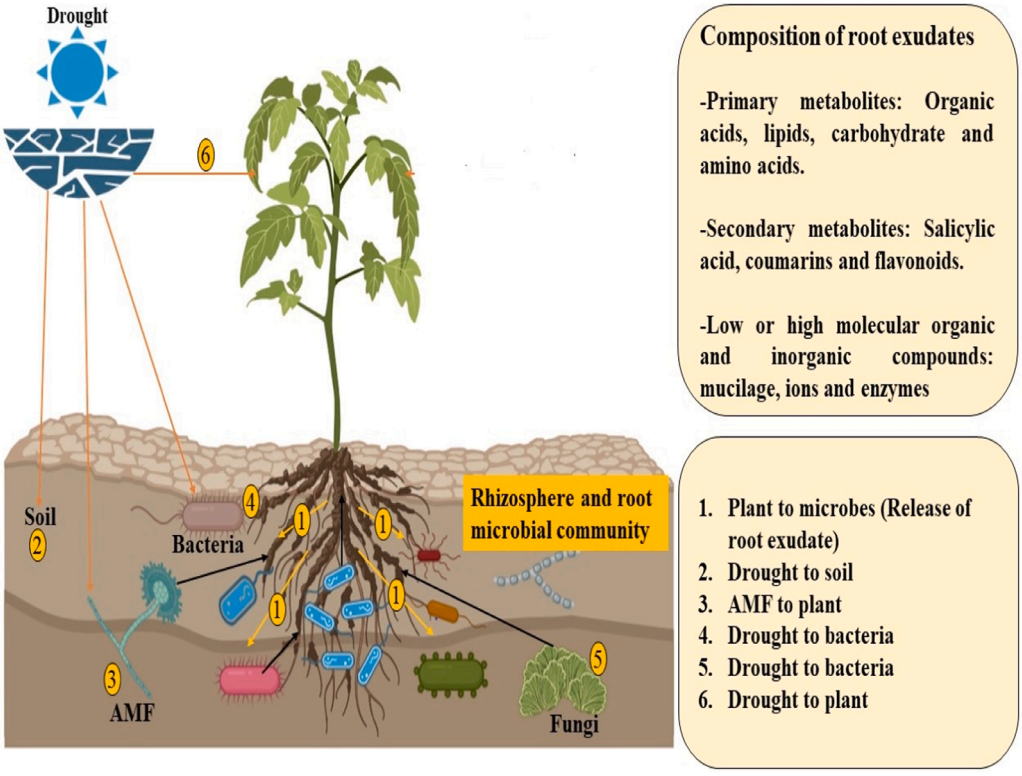

Fig. 2. Effects of drought stress on plant–microbiome interactions. Exposure to drought alters the activities of the microbial communities, the morphological and physiological status of the plant and microorganisms and the physicochemical properties of the soil.

downregulated in sorghum during drought stress (Xu et al., 2021). Also, It has been reported that the rice TOM1 gene encodes a phytosiderophore exporter called mutagenic acid, which makes it easier for soil to absorb iron (Nozoye et al., 2011). Specifically, for Actinobacteria, the population of rhizosphere bacteria in maize TOM1 mutants differed greatly from the wild type; although, during drought stress, only a little difference was seen between wild-type and tom1 plants (Xu et al., 2021). Furthermore, the enrichment of Actinobacteria taxa like Streptomyces caused by drought stress was interrupted by the external iron (Fe^{3+}) administration. Additionally, iron (Fe^{3+}) supplementation hindered Streptomyces spp ability to promote root development. All of these findings point to a reduced phytosiderophore production during drought, which either indirectly or directly leads to an increase in Actinobacteria sp like Streptomyces that support plant development exposed to drought. According to Tsai and Schmidt (2017), only graminaceous plants may use phytosiderophores, which begs the issue of whether nongraminaceous plants might also benefit from Streptomyces spp effect's on drought-induced plant growth enhancement.

Although the precise processes for reorganizing the population of microbes and consequences on the host remain mainly unclear, changes in the community of microorganisms during drought stress and after rewatering were also examined. After rewatering, the structure of the bacterial community in sorghum quickly (in about a week) recovered to that of a sample that had received adequate water (Xu et al., 2018). Due to its semi-aquatic growth pattern and thin root structure, rice is more vulnerable to drought stress than drought-tolerant sorghum (Ito et al., 1999). Even after rewatering over the entire life cycle, the bacterial population in rice plants exposed to extreme drought did not revert to the state of well-watered control (Santos-Medellın et al., 2021). It would be fascinating to find out how much the differences in regional soil, microbial composition or host genetics account for the differences in the capacity of rice and sorghum to restructure microbiota.

The next green revolution has been predicted to be based on crop microbiomes (Jez et al., 2016). Crop microbiomes have a significant impact on host performance, but the degree to which they do so is frequently strongly correlated with specific species and their relative abundances (Sieber et al., 2019). Understanding the mechanisms behind the processes by which crop-associated microbial communities are assembled is crucial (Trivedi et al., 2020; Babalola et al., 2020). In order to propose overarching concepts for plant microbiome research, ecological models have been created (Dini-Andreote and Raaijmakers, 2018). The effective delivery of inoculants to existing crop microbiomes depends on understanding the microbiome assembly mechanisms that occur throughout crop growth, which are currently mostly unexplored.

Additionally, the functionality and assembly of the microbiome may be impacted by the timing and order in which species arrive, or the priority impacts. An *Arabidopsis thaliana* gnotobiotic phyllosphere's community assembly is sensitive to priority effects, according to a recent study (Carlström et al., 2019). Some keystone species, such as Rhizobium, Microbacterium, Rhodococcus, and Sphingomonas, have the greatest capacity to change the community compositions. It is challenging to understand how priority effects in natural environments affect crop microbiome assembly and if these affects may last throughout the length of crop growth and generations because this field of study is still in its infancy. Adopting such knowledge might significantly increase our capacity to encourage the establishment of newly imported microbial strains and open the door to the promising prospect of designing specific crop microbiomes to enhance host performance.

3.1.2. Fungal community assembly

In general, the impacts of drought on the community structure of fungi around roots are less pronounced or even nonexistent (Furze et al., 2017; Ochoa-Hueso et al., 2018). Additionally, when faced with drought, fungal networks' cooccurrence remained more stable than the community of fungi (de Vries et al., 2018). However, other studies have found that drought has caused changes in the fungal population, especially in ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi, which are crucial for reducing the impact of drought by giving the host plant water and nutrients (Brunner et al., 2015; Talaat and Shawky, 2017). Drought can alter the community structure and colonization of ECM fungi, alter hyphae growth and production of arbuscule, and reduce the colonization of AM fungi (Compant et al., 2010; Omomowo et al., 2018). *C. geophilum* is a dominant species of ECM in certain naturally dry areas, including pine forests on seasonally dry wood, dunes and savannah (Matsuda et al., 2009). This is likely because *Cenococcum geophilum* has an increased level of tolerance to drought stress (Fernandez and Koide, 2013).

On seven grasslands across two continents, changes in the relative abundance of Basidiomycota and Ascomycota during drought was observed, and these changes were negatively connected with the amount of rainfall (Ochoa-Hueso et al., 2018). In response to drought, a shift in the fungus population was also noted in the endosphere of the root and rhizosphere of the rice plant (Santos-Medellín et al., 2017). Under well-watered, pre- and post-flowering conditions of drought, drought-sensitive and drought-tolerant sorghum were produced in the field, while the community of fungi throughout the growth stages of sorghum plant were examined (Gao et al., 2020). The plant genotype, plant developmental stage, and sample compartment all had an impact on the composition of the fungal communities, although stochasticity also seemed to be a major factor.

When plants were at an early embryonic stage and subjected to drought stress, stochastic pressures for the assembly of the community of fungi were significant, but after rewatering, no stochasticity was seen in the assembly of the community of fungi. This shows that when the abundance of fungi was low, stochasticity had a greater impact on the fungal communities. Furthermore, it appears that when the effects of the drought were removed, the host outweighed the stochastic assembly of the community of fungi. Uncertainty surrounds the origin of "stochasticity" on the assemblage fungal community in the plant; potential origins include stochastic plant development and physiological states, as well as stochastic impacts of drought on fungi.

3.2. Impact of drought stress on microbes, soil and plants

Reduced heat, precipitation, or fire-induced drought alters soil properties such as soil moisture, soil aggregation, nutrient dispersion and solubility, enzyme activity, and solute concentration (Schimel, 2018; Gupta et al., 2020, De la Fuente Cantó et al., 2020, Morcillo and Manzanera, 2021). Osmotic stress, water stress, nutritional stress, and salt stress, are only a few of the pressures that these variations produce in plants. As a result, drought is a multifaceted stress. To adapt to the water-scarce environment, plants undergo to changes into the root architecture, closing of the stomata, and a reduction in photosynthesis. Alongside a decrease in the rate of germination, a delaying reproduction time, and changes in the quantity and root exudate compositions (Gupta et al., 2020, De la Fuente Cantó et al., 2020, Fadiji et al., 2022a). Microbes' habitat, physiology, and activity are all impacted by drought condition. As a result, osmotic compound buildup increases, sporulation rate rises, enzymatic activities decline, nutrient cycling is reduced, and habitats shift. These may also result in modifications to the make-up of microbial communities (Jansson and Hofmockel, 2020; Morcillo and Manzanera, 2021). Changes in microbes, soil, and plants affect each other.

3.3. Notable factors affecting plant-microbe interactions under drought stress conditions

3.3.1. Root exudates

Root exudates, which can account for up to 40% of the carbons ingested during photosynthesis, are discharged into the soil (Fuentes et al., 2020; Bhattacharyya et al., 2021). Root exudates (e.g. organic acids, sugars, amino acids, etc.) act as signaling molecules, altering the

interactions between microorganisms and plants, among microbes-microbes and plants-plants. They also provide nutrients for microorganisms and shift the chemical and physical characteristics of the soil. Although monitoring root exudates during a drought has its technological limitations, variations in the volume and make-up of root exudates have been seen (Canarini et al., 2019; Fadiji et al., 2022b). As the severity of the drought increases, the total volume of root exudates is likely to decline while the allocation of the ratio of carbon to root exudates rises. However, amid the severe occurrence of drought stress, a different scenario occurred (Preece and Peñuelas, 2016).

The allocation of absorbed carbon to root, soil, shoot, and microorganisms during drought stress and rewatering was studied by Karlowsky et al. (2018). Drought increased the amount of carbon allocated to soil organic carbon and root sucrose. The result showed that the abundance of Actinobacteria rose during drought stress which is consistent with the finding that whereas the allocation of carbon to soil fungi and bacteria generally reduced during drought stress, allocation to Actinobacteria was not altered (Naylor et al., 2017). The carbon utilization was returned to normal throughout the recovery period. These findings imply that plants continue to secrete root exudates during drought stress to facilitate microbial activity recovery once rewatering has been initiated, which may aid in the recovery from drought stress in plants. The fact that the rate of soil respiration was greater in soil that had more root exudates from plants that had experienced drought compared to soil that had exudates from drought-unaffected plants supports this theory (De Vries et al., 2018). However, it is still unknown which elements of the root exudates cause an increase in soil respiration when exposed to drought.

Furthermore, when there is a drought, nutrient mobilization declines, making it challenging for organisms to absorb essential nutrients (Farooq et al., 2012). The nutrient cycle depends on substances released into the soil by microorganisms and plants, including sulfate, phosphorus, and nitrogen (Farooq et al., 2012). During drought stress, enzyme activity such as those of urease, protease, invertase, catalase and phosphatase change, which may have an impact on the nutritional status of the soil (Song et al., 2012). Organic acid exudation rates increased as osmotic pressure rose, and the increment rate was larger in maize that is tolerant to drought than in those that are sensitive to drought (Song et al., 2012). Increased levels of organic acids, particularly citrate, exposed to drought stress may lead to an increment in phosphorus mobilization, and nutrient stress reduction and possibly serve as one of the mechanisms by which maize plants are able to withstand drought because of the way that they affect phosphorus mobilization (Song et al., 2012).

3.3.2. Mucilage

When there is a drought, both plants and microorganisms depend on mucilage, a polymeric material secreted from plant cells like root cap cells that are mostly composed of polysaccharides and contain only a minor number of phospholipids and proteins (Read et al., 2003). High viscosity, low surface tension, and the ability to absorb significant amounts of water because of the polysaccharide's hydroxyl groups are all thought to be vital for the activities of the rhizosphere since they mitigate the severe environmental shift (Carminati et al., 2017; Zarebanadkouki et al., 2019). For example, during drought stress, the rhizosphere of *Lupinus albus* had more water than the bulk soil around it (Carminati et al., 2010).

Mucilage boosted the rhizosphere's ability to retain hydraulic conductivity, which would aid plants in absorbing water (Ahmed et al., 2014). Additionally, the addition of mucilage increased the tagged carbon diffusion in an artificial rhizosphere formed of extracted sand and mucilage, confirming the notion that mucilage facilitates the movement of nutrients during drought stress (Zarebanadkouki et al., 2019). Under drought and normal conditions, mucilage also boosted microbial biomass of the soil and the activity of enzymes such as chitinase, acid phosphatase and b-glucosidase (Ahmed et al., 2018). These methods are effective for comprehending how drought stress affects interactions between plants and microorganisms, but additional in-depth research employing plant genetics and in-plant conditions is needed before mucilage can be used in agricultural practice.

3.4. Impact of drought stress on plant-microbe interaction

Numerous bacteria help plants by altering how they react to drought. *Streptomyces* spp. enrichment on roots during exposure to drought stress in rice and sorghum has been the subject of multiple publications (Fitzpatrick et al., 2018; Santos-Medellın et al., 2021). Fitzpatrick et al. (2018) found a positive association between plant drought tolerance and the abundance of *Streptomyces* spp. in the bacterial population associated with the root, which suggests that enriching *Streptomyces* spp. may encourage plant development under drought conditions.

Much research has also been done on the application of microorganisms to lessen the impact of drought stress on plants. Under drought conditions, *Burkholderia phytofirmans* inoculation of field-cultivated wheat enhanced the rate of photosynthesis, water and nutrient absorption, and moisture content of the soil (Naveed et al., 2014). Under drought conditions, the bacteria *Ochrobactrum pseudogregnonense* and *Bacillus safensis* increased the antioxidant enzymes activity and enhanced wheat growth (Chakraborty et al., 2013). In *Arabidopsis thaliana*, and *Arabidopsis brasilense* boosted the important abiotic stress-associated phytohormone such as abscisic acid and improved tolerance to drought stress (Cohen et al., 2015). Yooyongwech et al. (2013) found that colonization of AM fungi increased the osmoprotectants' soluble sugar and proline content, stimulated the development of macadamia plants, and increased the permeability of water in maize during drought stress (Quiroga et al., 2019).

In transcriptomic research that examined 22 different accessions of rice with varying levels of tolerance to drought, the gene expressions involved in symbiosis with AMF and photosynthesis were higher in drought tolerant accessions, indicating that drought tolerance of rice related to the colonization of AMF shows an intra-species variation (Groen et al., 2022). These findings imply that certain microbial colonization enhances tolerance to drought, but the mechanism by which this occurs and if microbial colonization particularly operates during drought or generally enhances the health of the plant are yet unknown.

Exopolysaccharides (EPS), which are similar to the mucilage released by the plant, may also aid in reducing the effects of drought on plants (Naseem et al., 2018). Long-chain biosynthetic polymers, such as proteins, polysaccharides, nucleic acids and lipids, make up EPS (Flemming and Wingender, 2010). When there is a drought, EPS production increases and the EPS composition changes (Donot et al., 2012). Additionally, *Pseudomonas aeruginosa*-induced drought-induced maize growth was further encouraged by EPS (Naseem and Bano, 2014). Even though EPS have been linked to plant and microbes interactions during drought stress, further research is needed to determine the exact components and mechanism at play.

In certain instances, drought stress in lettuce and tomato caused the AM fungus *Rhizophagus irregularis* to colonize the roots, which relieved drought (Ruiz-Lozano et al., 2016). It is interesting to note that both drought stress and *R. irregularis* colonization increased the phytohormone strigolactone synthesis in tomatoes. Given that strigolactones are the host identification signals for AMF, this implies that strigolactones operate as a "call-for-help" signal and start a positive feedback loop for the colonization of *R. irregularis* colonization that increases plant tolerance to drought.

Similar to these direct connections, interactions that exist between bacteria and fungus may also be impacted by drought and play a key role in reducing the stress caused by drought on plants. It is hypothesized that root exudates of the plant are transported into the soil by fungus hyphae, encouraging the activities of bacteria (Paterson et al., 2016). It was also demonstrated that bacteria in situations with restricted access to water or nutrients might transfer carbon, nitrogen and water to other

bacteria. Direct nutrition and water transfer were observed, and the rate of vegetative development of *B. subtilis* was boosted when fungus hyphae connected to the spores of *B. subtilis* (Worrich et al., 2017). These instances highlight the significance of taking drought-related multitrophic interactions between plants, bacteria and fungus into account.

4. Salt stress

4.1. Impacts of salt stress on soil, microbes and plants

Salt has an impact on the chemical and physical make-up of the soil. Due to less soil aggregation than saline soil, which includes a variety of salts, sodic soil (the concentration of Na^+ is greater than 15%) leading to a weak soil structure. Low hydraulic permeability and conductivity characterize the sodic soil. Alkaline soil results from the adsorption of Na^+ to soil, which also raises the pH of the soil. Salt-induced soil property changes frequently impede plant development (Osman, 2018). Osmotic stress and ionic toxicity are the two basic stages of salt stress in plants. The first stage begins right away once the salt concentration surrounding the roots rises, causing osmotic stress and inhibiting water intake. The second phase begins gradually as the Na+ content in leaves rises.

A high Na^+ concentration in the cell prevents the absorption of other ions, disrupting metabolic processes and having a variety of negative consequences, including a decrease in the rate of photosynthetic activity. Secondary responses caused by osmotic and ionic stressors include Ca^{2+} signaling activation, reactive oxygen species (ROS) generation, and abscisic acid (ABA) buildup (Osman, 2018; Yang and Guo, 2018). The composition of root exudates and root architecture are impacted by salt stress (Gavelienė et al., 2022). Salt stress affects the structure and physiology of microbial communities, affecting things like soil respiration, microbial biomass, extracellular enzyme activity, and the mineralization of nitrogen and carbon (Singh, 2016). These in turn affect soil structure and plant physiology.

According to Julkowska and Testerink (2015) and Yang and Guo (2018), stress as a result of salt presence is a significant factor in crop loss. It is anticipated that due to natural factors and agricultural practices, the area occupied by salt-affected soils has been increasing by around 10% yearly (Shrivastava and Kumar, 2015). As compared to drought, salt stress is complicated since other pressures can cause it, and as a result, it often occurs in conjunction with similar stresses like heat and drought (Yensen, 2008) (Fig. 3).

4.2. Effects of salt stress on microbial community assembly

The dynamics of the microbial communities of salt-tolerant members and salt-sensitive of the family Cucurbitaceae exposed to salt stress were studied by Li et al. (2021). The result showed that in the rhizosphere of the salt-sensitive plants, but not salt-tolerant plants, the diversity of bacterial populations is reduced in response to the stress caused by the presence of salt, indicating that salt-tolerant plants maintain a diversified bacterial community that may be crucial for plant salt tolerance. Pseudomonas was more abundant in both plant types, even though distinct bacterial species were enriched in salt-tolerant and sensitive plants under salt stress. Importantly, the study demonstrated that regardless of plant salt sensitivity, microbes recruited by salt-treated plants increased the tolerance of the plant exposed to salt stress.

There are further publications on the dynamics of microbial communities exposed to salt stress. For example, in the groundnut rhizosphere, salt stress led to a proportionate rise in Acidobacteria and Cyanobacteria with a reduction in the abundance of Chloroflexi and Actinobacteria (Xu et al., 2020). In *Medicago truncatula*, salt stress caused alterations in the bacterial population, notably an increase in the abundance of *Enterobacter* species (Yaish et al., 2016). Even though, these findings indicate that plants use a particular microbial community to support their health of plants when under salt stress, an advance

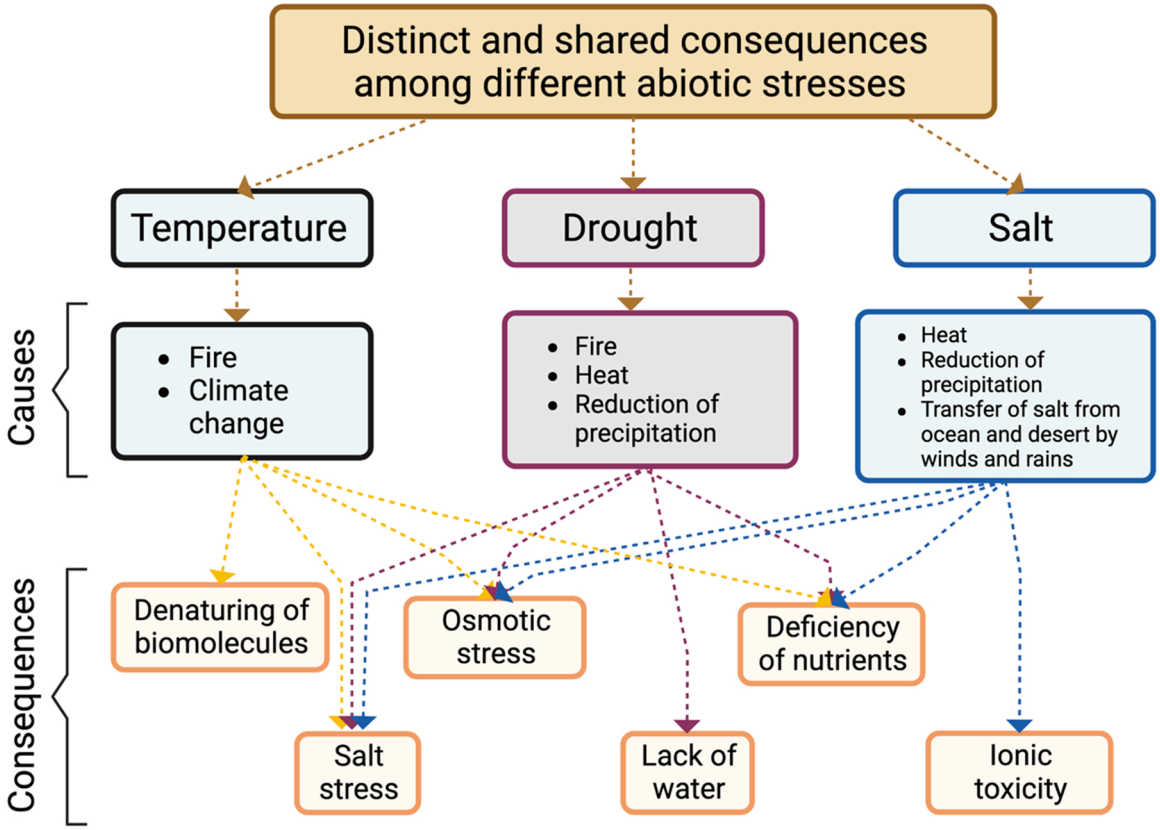

Fig. 3. Shared and independent consequences of drought, temperature and salt stresses on plant metabolism.

mechanistic and systematic investigation using various conditions of salt stress and plant species is necessary to fully comprehend the impact of salt stress on the microbiome associated with plants.

Salt stress causes changes in the community structure of bacteria both above and below ground (Hou et al., 2021b). In *A. thaliana* leaves, salt stress changes the abundance of a wide variety of bacteria from various phylogenetic lineages instead of just one taxonomic group (Berens et al., 2019). Furthermore, independent of salt stress, the formation of the bacterial microbiome was reliant on the age of the leaf. Majorly, mutant and wild-type plants lacking in phytohormones such as salicylic acid (SA), and the abscisic acid (ABA) pathway displayed different community shifts in response to salt stress, showing that salt stress-triggered alterations in the community of bacteria depend on the genotype of the plant. These findings imply that phytohormones like ABA and salicylic acid (SA) coordinate the formation of salt stress and leaf age-dependent microbiota (Berens et al., 2019).

4.3. Impacts of salt stress on plant-microbe interaction

Under salt stress, microorganisms can indirectly or directly impact a plant's physiological condition by altering ion concentrations within and outside of the plant, phytohormone signaling, nutrient and water intake, as well as soil characteristics (Osman, 2018). Many processes can be active at once, and it's sometimes difficult to understand how they interact. Fig. 4 provides an overview of how salt stress affects the interactions between plants and microbes.

4.3.1. Ion concentration changes

Under both normal and salt stress conditions, the development of *A. thaliana* was aided by volatiles from *B. subtilis*, and the expression of the high-affinity K^+ transporter 1 (HKT1) in the shoots and roots changed in opposite directions (Zhang et al., 2008). Plants inoculated with *B. subtilis* volatiles showed consistently lower Na^+ and higher K^+ levels. These HKT1-required *B. subtilis* volatiles exposed to salt stress is needed for plant growth-promoting activities (Zhang et al., 2008). Taken together, these findings indicates that the volatiles of *B. subtilis* suppress the expression of HKT1 in the roots while causing an increment in shoots to reduce the entry of Na^+ to roots and enhancing shoot-to-root recirculation of Na^+. This finding is consistent with prior research on HKT1 functions in Na^+ export in shoots and import into the roots of the plant (Davenport et al., 2007). In white clover, a comparable finding was made (Han et al., 2014). It is yet unknown the way *B. subtilis* or plant regulates the expression of HKT1 in a tissue-specific way or how Na^+ recirculation works in detail at the molecular level.

By lowering rhizosphere Na^+ concentrations, EPS produced by bacteria has been hypothesized to provide plants with the ability to tolerate salt stress (Arora et al., 2010; Kasotia et al., 2016). Salt stress changed the quantity and composition of EPS (Nunkaew et al., 2015). Additionally, EPS play additional functions in the production of biofilms and soil aggregation, both of which have an impact on plants. Therefore, the next studies should look at specific processes such as how Na^+ would be absorbed by EPS and the proportional impacts of various exopolysaccharides on plant resistance to salt stress.

4.3.2. Modification of phytohormone signaling

The ethylene (ET) phytohormone precursor, which controls plant yield, stress response and growth, is 1-aminocyclopropane-1-carboxylate (ACC). ACC oxidase changes ACC into ET. Microbes' ACC deaminases convert ACC to a-ketobutyrate and NH_4^+ (Changhong et al., 2012). Numerous studies have reported that bacteria capable of producing ACC deaminases stimulate plant growth when faced with environmental stressors like drought and salt (Del Carmen Orozco-Mosqueda et al., 2020). Plant leaves, roots, and seeds exude ACC, which certain bacteria utilize as a source of nitrogen (Glick, 2014). Bacteria with ACC deaminase can promote plant growth and help to feed the world.

Reduced ACC outside plants are thought to encourage exudation of

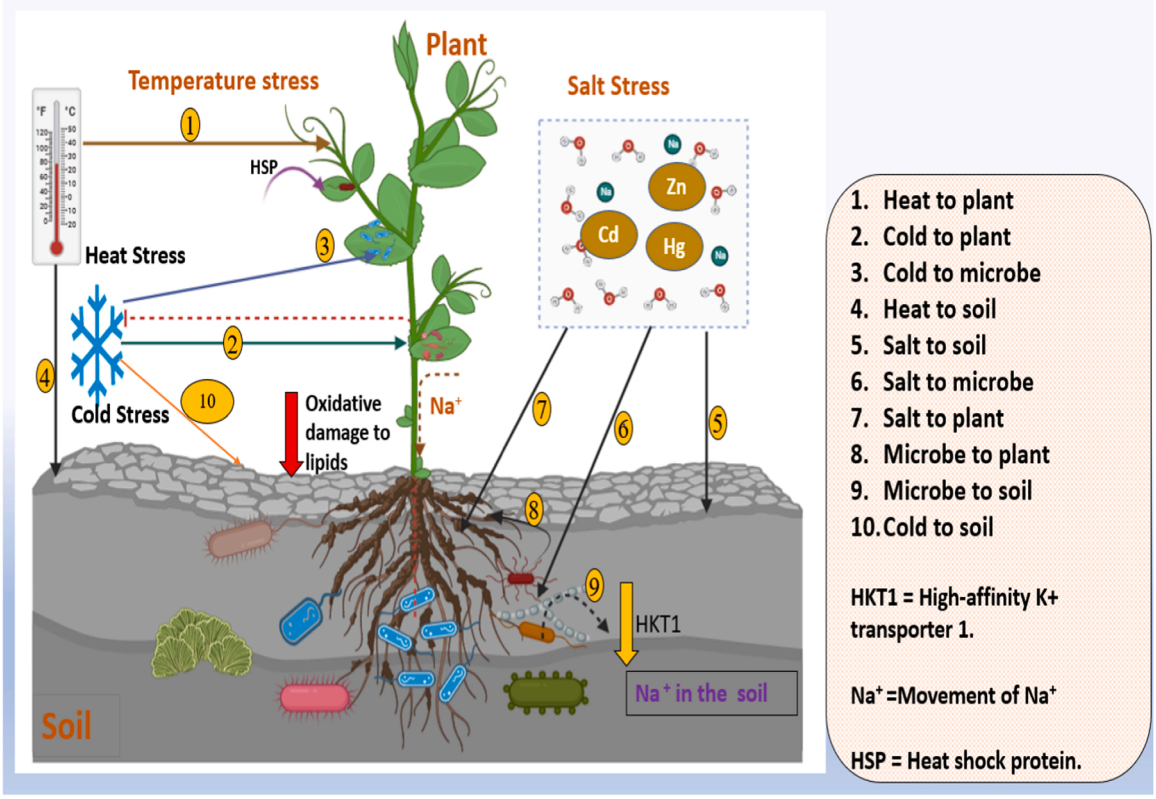

Fig. 4. Effects of temperature and salt on plant-microbiome interactions. Exposure to temperature and salt alter microbiome, the morphology and physiological state of microorganisms. It also affects the interactions between plants and microorganism as well as the soil's physicochemical properties.

ACC, which in turn lowers ACC accumulation and ET generation in plants, enhancing the growth of the plant (Glick, 2014; Singh et al., 2015). However, this hypothesis lacks clear experimental support. According to biochemical and phylogenetic studies, ACC deaminases are broadly dispersed across microorganisms, not just those linked with plants (Singh et al., 2015). As a result, different plant-microbe pairings may result in different plant-microbe interactions via ACC deaminases. More research is thus required, such as evaluating the variations and similarities in interactions between plants and microorganisms through ACC deaminases.

In a novel method described by De Zelicourt et al. (2018), 2-keto-4--methylthiobutyric acid (KMBA), an ET precursor released by *Enterobacter* sp. SA187 isolated from *Ipomoea argentea* enhanced the development of *alfalfa* (*Medicago sativa* L.) and *A. thaliana* which was linked to a higher K+ /Na+ ratio in the roots and shoot of the plant. In particular, the impact of *Enterobacter* sp. SA187 on plant growth promotion was reduced in A. mutant plants from the *A. thaliana* genus that lack ET signaling but not ET biosynthesis. In *Enterobacter* sp. SA187, genes involved in the KMBA pathway were expressed more often in *A. thaliana*. When used alone, KMBA imitated *Enterobacter* sp. advantageous traits. The positive effects of *Enterobacter* sp. SA187 were lost as a result of the inhibition of KMBA (De Zelicourt et al., 2018).

These findings imply that salt stress-induced plant development was aided by ET synthesis by *Enterobacter* sp. SA187 via KMBA. This defies the accepted theory that ACC deaminases generated by bacteria stimulate plant growth. It is necessary to conduct more studies on the effects of ET and ACC on tolerance to salt stress that is mediated by microorganisms. In more recent research, it was demonstrated that *Enterobacter* sp. SA187 saved *A. thaliana* that were showing signs of sulfur deficiency when exposed to salt stress (Andres-Barrao et al., 2021). The whole sulfur metabolic pathway of *Enterobacter* sp. SA187 was also elevated following *A. thaliana* colonization, indicating that bacteria and plants work together to increase plant tolerance to stress tolerance through coordination of the sulfur metabolic pathways. This discovery also reveals a molecular connection to KMBA-mediated enhancement of plant growth when exposed to salt stress since plant ET signaling controls the sulfur regulon for sulfate absorption and synthesis of amino acids containing sulfur (De Zelicourt et al., 2018).

It is important to note that certain bacteria generate a variety of phytohormones that might influence the tolerance of the plant to salt stress, including auxins, cytokinins, ABA, SA, and gibberellins. Exogenous administration of SA has been shown to increase salt stress tolerance (Mohamed et al., 2011; Fadiji et al., 2021a; Fadiji et al., 2021b), and SA-producing microorganisms can also improve tolerance to salt stress (Forchetti et al., 2010; Fadiji and Babalola, 2020a). These suggest that SA produced by microorganisms may contribute to increased plant tolerance to salt stress. Direct evidence for the impact of SA generated by microbes on plant salt tolerance, however, is currently absent. According to several studies, the inoculation of phytohormone-producing bacteria modifies how plants react to different stimuli, which can either increase or decrease a plant's tolerance to stress (Egamberdieva et al., 2017). We presently know very little about the molecular effects of phytohormones generated by microbes on the physiology of the plant and tolerance to abiotic stresses. This holds for all pressures, not only salt stress. It is necessary to investigate the mechanism plants used to endure stress mediated by phytohormones secreted by microbes.

5. Temperature stress

5.1. Impact of temperature stress on microbes, plants, and soil

The temperature in the atmosphere has an impact on the soil's pH, moisture content, nutrient diffusion and aggregation (Onwuka and Mang, 2018). Plants and microorganisms are also affected by these modifications (Onwuka and Mang, 2018). Numerous plant metabolic processes are altered by heat stress, including the buildup of ROS, modification of phytohormone signaling, reduction of the rate of respiration and photosynthesis, proteins inactivation, cellular membranes permeability and alteration of fluidity (Zhao et al., 2020). Plants are also impacted by cold stress (Dai et al., 2019). Effects vary according to plant species, other environmental factors, stress level, frequency, and duration. These modifications affect how plants develop and grow, which frequently reduces agricultural production (Dai et al., 2019; Zhao et al., 2020).

The structural and chemical make-up of nucleic acids, proteins, and membranes in microbes are altered by temperature changes (Rajasheker et al., 2019; Zhang and Gross, 2021), which has an impact on physiological activities of microorganisms. Our understanding of temperature impacts on plant-microbe interactions as compared to salt and drought stress is limited, even though the impact of temperature stress on the interaction between plants and microorganisms has been widely studied. Additionally, additional stressors including temperature stress are connected.

5.2. Impact of temperature on the assembly of microbial community

The bacterial population of the sorghum root was studied by Wipf et al. (2021) in relation to the impacts of combined heat and drought stresses. Even though individual drought and heat stress enhanced the population of the Actinobacteria and decreased the population of Proteobacteria in soil and roots, specific Actinobacteria were enriched for heat and drought, indicating that sorghum recruits numerous microbiomes when exposed to heat and drought stress. To further understand how various bacteria are attracted to plants and how these microbial assemblages affect a plant's ability to withstand heat stress, more research is required.

5.3. Impact of temperature on plant-microbe interactions

5.3.1. Stress from high temperature

According to some findings, microorganisms help plants tolerate heat better. The mechanisms for this improvement include increased plant nutrient absorption and growth as well as detoxification of ROS, which reduces the damage to the cell (Khan et al., 2020a; Shekhawat et al., 2021). For example, both in hot and normal conditions, *B. cereus* boosted chlorophyll content and growth of soybean. Heat-induced increment in ABA and reduction in SA were mitigated by *B. cereus* injection (Khan et al., 2020a). Improved cyclamen heat tolerance following inoculation with the AM fungus *Glomus fasciculatum* was linked to an increment in antioxidative activity (Maya and Matsubara, 2013). These findings indicate the possibility of bacteria promoting tolerance of the plant tolerance to heat, although the exact mechanism by which microbes do so is still largely unknown.

Recently, a method of bacteria-induced heat tolerance was described by Shekhawat et al. (2021). The laboratory- and open-field-grown wheat plants were more tolerant of heat after receiving an inoculation of the endophytic bacteria, *Enterobacter* sp. SA187. via modifying the trimethylation of lysine 4 on histone H3 (H3K4me3), which is a constitutive change, in the promoter genes involved in heat-stress HSP18.2 and APX2. SA187-induced thermotolerance in *A. thaliana* was shown to be mediated by ET signaling. These epigenetic changes would prime, but not necessarily activate, a heat stress response that is harmful to plant development. These show how useful root endophytes are for improving the ability of agricultural crops to withstand heat stress. ET signaling contributes to the ability of rice and tomato to withstand heat stress (Pan et al., 2019). These findings provide credence to ET's involvement in SA187-induced thermotolerance. The enhanced heat tolerance of *A. thaliana* mutant plants, however, suggests that ET has a detrimental effect on plants' tolerance to heat stress (Clarke et al., 2009). These point to a sophisticated mechanism for tolerance to heat including ET signaling.

5.3.2. Stress from low temperature

Additionally, the microorganism can improve a plant's resistance to cold. Some changes in the physiology of the plant related to microbial inoculation have been described, despite poorly understood processes. For instance, *Burkholderia phytofirmans* inoculation increased carbon fixation and increased the accumulation of starch, proline, carbohydrates, and phenolics in grapevines, promoting cold tolerance (Theocharis et al., 2012). The sensitivity of plants to cold stress was likewise boosted by AM fungus (Caradonia et al., 2019). For instance, under normal and cold-stress exposures, the inoculation of tomatoes with *Glomus mosseae* improved the plant's growth, activities of antioxidative enzyme and chlorophyll content. Malondialdehyde buildup brought on by cold was reduced by *Glomus mosseae* inoculation, indicating that *Glomus mosseae* lessens the damage caused to lipids brought on by exposure to cold environments (Abdel Latef and Chaoxing, 2011).

According to Shivaji and Prakash (2010), the rigidity of the membrane seems to be one of the initial signals that are perceived by bacteria when they are under stress caused by low temperatures. Signal perception and transduction then occurs via a two-component signal transduction pathway, consisting of a membrane-associated sensor and a cytoplasmic response regulator, and as a consequence, a set of regulated genes are activated due to low temperature stress. Some temperature regulators such as Rer26 and Hik33 are involved in cold signaling in cyanobacteria such as *Synechocystis*, while others, such as DesK and DesR, participate as a sensor and the response regulator, respectively, in bacteria such as *Bacillus subtillis*. Likewise, there are changes in the DNA topology due to temperature changes, which can trigger cold response actions (Shivaji and Prakash, 2010).

It has been observed that the production of disaccharides such as trehalose, which is also involved in resistance to water stress, drought, among others, is also important in maintaining the rigidity and stability of the membranes in *E. coli* (Kandror et al., 2002). Therefore, their production under cold stress is essential to maintain viability and survival.

6. Tolerance mechanisms used in beneficial plant-microbe interactions

Endophytes throughout their entire lifecycles, coexist with plants in symbiotic interactions. Endophytes often colonize plant tissues by entering the seeds, roots, leaves, and stems of their host plant. By enhancing the fixation of nitrogen, the release of phytohormones, and the uptake of nutrients, they may enhance plant development. Entophytic microorganisms obtain their energy from the root exudates that plants secrete (Thakuria et al., 2004). The production of exopolysaccharides by bacterial cells during the early phases of colonization helps to shield those cells from oxidative damage (Chandra et al., 2007). Arbuscular mycorrhizal fungus have considerably improved the plant's ability to absorb nutrients and to withstand abiotic stressors. The symbiotic relationship between AMFs and their host plants controls plant development and growth. The intricate AMF mycelial network around the roots has boosted nutrient intake as well. A common mycorrhizal network (CMN) has a favorable impact on the translocation of nitrogen (N) and phosphorus (P), which in turn promotes plant development in harsh environmental circumstances (Muratova et al., 2005; Munir et al., 2022). Through interactions between plants and microbes, plants have developed biochemical and molecular processes that lessen the detrimental impacts of abiotic stressors on plant development. Numerous phytohormones, including as cytokinins, gibberellins, and auxins, have changed the root shape, eventually enabling the plant to withstand harsh climatic circumstances (Accumulation of heavy-metal, salt stress, drought, accumulation, and nutrient deficiency).

Abiotic stressors' harmful effects can be significantly reduced because of induced systemic tolerance (IST). Plants may withstand environmental challenges due to the synthesis of phytohormones like abscisic acid, cytokinins, and IAA for instance. Additionally, the production of antioxidants like peroxidase (POD), superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX) and catalase (CAT), aids in reducing the negative effects of abiotic stresses as well as bacterial ACC deaminase's degradation of the ethylene precursor (Beneduzi et al., 2008). Inoculating plants with PGPRs capable of producing the enzyme 1-aminoacylcyclopropane-1-carboxylate (ACC) deaminase, which catalyses the conversion of ACC into alpha-ketobutyrate and ammonia, is another way to lessen the detrimental effects of abiotic stressors (Roesti et al., 2006). Increases in low-molecular-weight osmolytes such glycine betaine, proline, amino acids, organic substances, and several other enzymes (such as glucanase, ACC-deaminase and chitinase) can aid in the growth and development of plants under abiotic stress (Dimkpa et al., 2008). AMFs have been shown to be effective in reducing abiotic stress in plants through a variety of mechanisms, including increased osmotic adjustment, accumulation of proline, downregulation of stress-related genes, jasmonic acid, high glutathione levels, and increased synthesis and expression of stress resistance genes to strengthen the defense system (Khan et al., 2020b).

7. Future outlook

Even though we now have a better understanding of how plants and microorganisms interact under the focused abiotic stresses, there are still many crucial issues that need to be answered. Mechanistic knowledge encompasses a wide range of scientific areas, from the molecular level to the ecological level. Advanced technologies including metatranscriptomics, metagenomics, plant-colonizing bacteria and temporal-spatial mapping of the responses of the plant must be combined with this research. Animal microbiota research has produced a number of groundbreaking studies (Shi et al., 2020), but plant microbiota research still requires technical advancement.

The bulk of mechanistic research relies on monoassociation, however, in nature, plants interact with a variety of microorganisms at the same time. Studies on the mechanistic level of interactions between plants and bacteria are often quite a few. Plant-microbiota interactions can be built upon the findings of monoassociation research, although it is unclear how these findings may be used to explain plant-microbiota interactions. There is a need for more organized research employing synthetic communities (SynCom) in community contexts. SynCom systems have been developed for rice (Voges et al., 2019; Harbort et al., 2020) and *A. thaliana* (Voges et al., 2019; De Souza et al., 2020). We still require more diverse SynCom systems, to uncover the fundamentals of plant-microbiome interactions.

Numerous studies have examined changes in the microbial community's relative abundance. While knowledge of microbial abundance is vital, it's equally crucial to understand how the absolute abundance of bacteria fluctuates in various organs and environments. Host-associated microbe PCR, a recent technical development, allows for the simultaneous measurement of relative changes in plant microbiome (Lundberg et al., 2021). Additionally, changes in microbial activity and spatial patterns of microbial colonization are just as relevant for comprehending the mechanisms of microbial impacts on plants as well as changes in microbial abundance. Furthermore, we require more high-resolution explanations of how environmental changes affect microbial abundance or depletion. For instance, the phylum Actinobacteria is made up of several families and species, even though various studies have shown the enrichment of Actinobacteria under drought stress. Since microorganisms' functions are frequently species- and strain-specific, higher resolutions and thorough classifications are required.

Applied research is mostly where mechanistic comprehension of microbial impacts on plants comes from. As a result, they don't always cohabit in nature. This needs to be remembered. Additionally, several processes are at work in various interactions between plants and microbes. In actuality, ACC deaminases is encoded in a wide variety of species, such as fungi, eukaryotes, and bacteria, and they have different regulations in each of these groups of organisms (Singh et al., 2015).

Furthermore, because plants are frequently subjected to a variety of abiotic stressors in the environment, it is challenging to evaluate how stress affects the plant microbiome. Reductionist methods in a carefully monitored laboratory experiment or with SynComs would offer mechanistic and functional insights into the way abiotic stresses affect the plant-microbiome relationship as well as how microbes affect a plant's ability to withstand abiotic stresses (Liu et al., 2019).

High levels of heterogeneity can be found inside a plant, and the response of the plant like gene expression is influenced by plant age, cell type, and tissue (Berens et al., 2019; Emonet et al., 2021). Plant age and tissue of the plant also affect microbiota assembly (Tkacz et al., 2020; Given et al., 2020). Future research should take into account the heterogeneous nature of the interactions between plants and microbiomes under abiotic stress.

Additionally, the different types of stress factors, such as drought, salinity and temperature that are reviewed here, there are other abiotic factors such as extremes of pH, the presence of heavy metals, etc. Therefore, they are generally analyzed separately, but in nature two or more of them can act and impact the survival of microorganisms, plants and soil health. Therefore, it would be good to further explore this multifactoriality within a global scheme or to see more from further afield the painting of the different biotic and abiotic relationships.

8. Conclusion

Even while we focused on fungi and bacteria in this study, interactions between plants and their microbiota also involve several other species, including archaea, oomycetes, viruses, nematodes and insects (Sánchez-Cañizares et al., 2017). For instance, viruses affect how well plants tolerate heat, and the long-term impact of drought on interactions between plants and viruses was also covered (Anfoka et al., 2016). Importantly, different microbes interact with one another and the host in holobiont nature. A balance between reductionist and holistic methods is therefore needed in order to fully grasp complicated relationships. Although pattern recognition receptors that sense chemicals produced by microbes or plants impart salt tolerance, SA signaling can adversely influence plant salt tolerance through crosstalk with ABA signaling. Immunity of the plant presumably has a significant influence on plant-microbiome interactions when exposed to different abiotic stresses, given that it is essential for managing and monitoring plant microbiota (Nejat and Mantri, 2017).

Despite the numerous reports of several beneficial benefits caused by microorganisms (see references cited in this work), our knowledge of the underlying molecular mechanisms is somewhat restricted. Customized agricultural solutions can be created if we have a mechanistic knowledge of the interactions between plants and microorganisms under diverse abiotic stress situations. To do this, a data-driven strategy utilizing machine learning would aid us in the development of solutions and models to address agricultural difficulties brought on by abiotic pressures by utilizing plant microbiota.

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CRediT authorship contribution statement

AEF and OOB conceived the ideas, collected the data, and developed the manuscript. ANY and GS provided professional input, proofread and reviewed the work. All authors approved the submitted version.

Conflict of interest

The authors declare that there is no conflict of interest.

Data Availability

No data was used for the research described in the article.

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References

Abdel Latef, A. a H., Chaoxing, H., 2011. Arbuscular mycorrhizal influence on growth, photosynthetic pigments, osmotic adjustment and oxidative stress in tomato plants subjected to low temperature stress. Acta Physiol. Plant 33, 1217–1225.
Abdelraheem, A., Esmaeili, N., O'connell, M., Zhang, J., 2019. Progress and perspective on drought and salt stress tolerance in cotton. Ind. Crops Prod. 130, 118–129.
Ahmed, M.A., Kroener, E., Holz, M., Zarebanadkouki, M., Carminati, A., 2014. Mucilage exudation facilitates root water uptake in dry soils. Funct. Plant Biol. 41, 1129–1137.
Ahmed, M.A., Sanaullah, M., Blagodatskaya, E., Mason-Jones, K., Jawad, H., Kuzyakov, Y., Dippold, M.A., 2018. Soil microorganisms exhibit enzymatic and priming response to root mucilage under drought. Soil Biol. Biochem. 116, 410–418.
Andres-Barrao, C., Alzubaidy, H., Jalal, R., Mariappan, K., De Zelicourt, A., Bokhari, A., Artyukh, O., Alwutayd, K., Rawat, A., Shekhawat, K., Almeida-Trapp, M., Saad, M., Hirt, H., 2021. Coordinated bacterial and plant sulfur metabolism in Enterobacter sp. SA187-induced plant salt stress tolerance. Proc. Natl. Acad. Sci. U. S. A. 118, e2107417118.
Anfoka, G., Moshe, A., Fridman, L., Amrani, L., Rotem, O., Kolot, M., Zeidan, M., Czosnek, H., Gorovits, R., 2016. Tomato yellow leaf curl virus infection mitigates the heat stress response of plants grown at high temperatures. Sci. Rep. 6, 1–13.
Arora, M., Kaushik, A., Rani, N., Kaushik, C., 2010. Effect of cyanobacterial exopolysaccharides on salt stress alleviation and seed germination. J. Environ. Biol. 31, 701–704.
Babalola, O.O., Fadiji, A.E., Ayangbenro, A.S., 2020. Shotgun metagenomic data of root endophytic microbiome of maize (Zea mays L.). Data Br. 31, 105893.
Bahar, A.A., Faried, H.N., Razzaq, K., Ullah, S., Akhtar, G., Amin, M., Bashir, M., Ahmed, N., Wattoo, F.M., Ahmar, S., 2021. Potassium-induced drought tolerance of potato by improving morpho-physiological and biochemical attributes. Agronomy 11, 2573.
Bakker, P.A., Doornbos, R.F., Zamioudis, C., Berendsen, R.L., Pieterse, C.M., 2013. Induced systemic resistance and the rhizosphere microbiome. Plant Pathol. J. 29, 136.
Beneduzi, A., Peres, D., Vargas, L.K., Bodanese-Zanettini, M.H., Passaglia, L.M.P., 2008. Evaluation of genetic diversity and plant growth promoting activities of nitrogen-fixing bacilli isolated from rice fields in South Brazil. Appl. Soil Ecol. 39, 311–320.
Berens, M.L., Wolinska, K.W., Spaepen, S., Ziegler, J., Nobori, T., Nair, A., Krüler, V., Winkelmüller, T.M., Wang, Y., Mine, A., 2019. Balancing trade-offs between biotic and abiotic stress responses through leaf age-dependent variation in stress hormone cross-talk. Proc. Natl. Acad. Sci. U. S. A. 116, 2364–2373.
Bhat, M.A., Kumar, V., Bhat, M.A., Wani, I.A., Dar, F.L., Farooq, I., Bhatti, F., Koser, R., Rahman, S., Jan, A.T., 2020. Mechanistic insights of the interaction of plant growth-promoting rhizobacteria (PGPR) with plant roots toward enhancing plant productivity by alleviating salinity stress. Front Microbiol 11, 1952.
Bhattacharyya, A., Pablo, C.H., Mavrodi, O.V., Weller, D.M., Thomashow, L.S., Mavrodi, D.V., 2021. Rhizosphere plant microbe interactions under water stress. In: Gadd, G.M., Sariaslani, S. (Eds.), Advances in Applied Microbiology, Volume 115. Elsevier, Academic Press, Cambridge, MA, U.S.A, pp. 65–113.
Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C., 2015. How tree roots respond to drought. Front. Plant Sci. 6, 547.
Canarini, A., Kaiser, C., Merchant, A., Richter, A., Wanek, W., 2019. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front. Plant Sci. 10, 157.
Canarini, A., Schmidt, H., Fuchslueger, L., Martin, V., Herbold, C.W., Zezula, D., Gündler, P., Hasibeder, R., Jecmenica, M., Bahn, M., 2021. Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. Nat. Commun. 2, 1–14.
Caradonia, F., Francia, E., Morcia, C., Ghizzoni, R., Moulin, L., Terzi, V., Ronga, D., 2019. Arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria avoid processing tomato leaf damage during chilling stress. Agronomy 9, 299.
Carlström, C.I., Field, C.M., Bortfeld-Miller, M., Müller, B., Sunagawa, S., Vorholt, J.A., 2019. Synthetic microbiota reveal priority effects and keystone strains in the Arabidopsis phyllosphere. Nat. Ecol. Evol. 3, 1445–1454.
Carminati, A., Moradi, A.B., Vetterlein, D., Vontobel, P., Lehmann, E., Weller, U., Vogel, H.-J., Oswald, S.E., 2010. Dynamics of soil water content in the rhizosphere. Plant Soil 332, 163–176.
Carminati, A., Benard, P., Ahmed, M.A., Zarebanadkouki, M., 2017. Liquid bridges at the root-soil interface. Plant Soil 417, 1–15.
Chakraborty, U., Chakraborty, B., Chakraborty, A., Dey, P., 2013. Water stress amelioration and plant growth promotion in wheat plants by osmotic stress tolerant bacteria. World J. Microbiol. Biotechnol. 29, 789–803.

Chandra, S., Choure, K., Dubey, R.C., Maheshwari, D.K., 2007. Rhizosphere competent Mesorhizobiumloti MP6 induces root hair curling, inhibits Sclerotinia sclerotiorum and enhances growth of Indian mustard (*Brassica campestris*). Braz. J. Microbiol. 38, 124–130.

Changhong, G., Jiali, L., Yueping, L., 2012. Isolate and characterize acc deaminase-containing plant growth-promoting rhizobacteria. In: Zhu, E., Sambath, S. (Eds.), Information technology and agricultural engineering. Advances in intelligent and soft computing, vol 134. Springer, Berlin, Heidelberg, pp. 241–247. https://doi.org/10.1007/978-3-642-27537-1_30.

Cheng, Y.T., Zhang, L., He, S.Y., 2019. Plant-microbe interactions facing environmental challenge. Cell Host Microbe 26, 183–192.

Chialva, M., Lanfranco, L., Bonfante, P., 2022. The plant microbiota: composition, functions, and engineering. Curr. Opin. Biotechnol. 73, 135–142.

Clarke, S.M., Cristescu, S.M., Miersch, O., Harren, F.J., Wasternack, C., Mur, L.A., 2009. Jasmonates act with salicylic acid to confer basal thermotolerance in *Arabidopsis thaliana*. N. Phytol. 182, 175–187.

Cohen, A.C., Bottini, R., Piccoli, P., 2015. Role of abscisic acid producing PGPR in sustainable agriculture. In: Maheshwari, D.K. (Ed.), Bacterial Metabolites in Sustainable Agroecosystem. Springer International Publishing, Cham, pp. 259–282.

Compant, S., Van Der Heijden, M.G., Sessitsch, A., 2010. Climate change effects on beneficial plant–microorganism interactions. FEMS Microbiol Ecol. 73, 197–214.

Compant, S., Samad, A., Faist, H., Sessitsch, A., 2019. A review on the plant microbiome: ecology, functions and emerging trends in microbial application. J. Advan. Res. 19, 29–37.

Cramer, G.R., Urano, K., Delrot, S., Pezzotti, M., Shinozaki, K., 2011. Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol. 11, 1–14.

Dai, L., Zhang, G., Yu, Z., Ding, H., Xu, Y., Zhang, Z., 2019. Effect of drought stress and developmental stages on microbial community structure and diversity in peanut rhizosphere soil. Int. J. Mol. Sci. 20, 2265.

Davenport, R.J., Muñoz-Mayor, A., Jha, D., Essah, P.A., Rus, A., Tester, M., 2007. The Na + transporter AtHKT1; 1 controls retrieval of Na+ from the xylem in Arabidopsis. Plant Cell Environ. 30, 497–507.

De La Fuente Cantó, C., Simonin, M., King, E., Moulin, L., Bennett, M.J., Castrillo, G., Laplaze, L., 2020. An extended root phenotype: the rhizosphere, its formation and impacts on plant fitness. Plant J. 103, 951–964.

De Souza, R.S.C., Armanhi, J.S.L., Arruda, P., 2020. From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. Front. Plant Sci. 11, 1179.

De Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., 2018. Soil bacterial networks are less stable under drought than fungal networks. Nat. Commun. 9, 1–12.

De Zelicourt, A., Synek, L., Saad, M., Alzubaidy, H., Jalal, R., Xie, Y., AndrEs-Barrao, C., Rolli, E., Guerard, F., Mariappan, K., Daur, I., Colcombet, J., Benhamed, M., Depaepe, T., Van Der Straeten, D., Hirt, H., 2018. Ethylene induced plant stress tolerance by Enterobacter sp. SA187 is mediated by 2-keto-4-methylthiobutyric acid production. PLoS Genet. 14, e1007273.

Del Carmen Orozco-Mosqueda, M., Glick, B.R., Santoyo, G., 2020. ACC deaminase in plant growth-promoting bacteria (PGPB): an efficient mechanism to counter salt stress in crops. Microbiol. Res. 235, 126439.

Dimkpa, C., Svatoš, A., Merten, D., Büchel, G., Kothe, E., 2008. Hydroxamate siderophores produced by *Streptomyces acidiscabies* E13 bind nickel and promote growth in cowpea (*Vigna unguiculata* L.) under nickel stress. Can. J. Microbiol. 54, 163–172.

Dini-Andreote, F., Raaijmakers, J.M., 2018. Embracing community ecology in plant microbiome research. Trends Plant Sci. 23, 467–469.

Donot, F., Fontana, A., Baccou, J., Schorr-Galindo, S., 2012. Microbial exopolysaccharides: main examples of synthesis, excretion, genetics and extraction. Carbohydr. Polym. 87, 951–962.

Egamberdieva, D., Wirth, S.J., Shurigin, V.V., Hashem, A., Abd_Allah, E.F., 2017. Endophytic bacteria improve plant growth, symbiotic performance of chickpea (*Cicer arietinum* L.) and induce suppression of root rot caused by *Fusarium solani* under salt stress. Front. Microbiol. 8, 1887.

Emonet, A., Zhou, F., Vacheron, J., Heiman, C.M., Tendon, V.D., Ma, K.-W., Schulze-Lefert, P., Keel, C., Geldner, N., 2021. Spatially restricted immune responses are required for maintaining root meristematic activity upon detection of bacteria. Curr. Biol. 31 (1012–1028), e7.

Fadiji, A.E., Babalola, O.O., 2020a. Exploring the potentialities of beneficial endophytes for improved plant growth. Saudi J. Biol. Sci. 27, 3622–3633.

Fadiji, A.E., Babalola, O.O., 2020b. Metagenomics methods for the study of plant-associated microbial communities: A review. J. Microbiol. Methods 170, 105860.

Fadiji, A.E., Ayangbenro, A.S., Babalola, O.O., 2021a. Shotgun metagenomics reveals the functional diversity of root-associated endophytic microbiomes in maize plant. Curr. Plant Biol. 25, 100195.

Fadiji, A.E., Ayangbenro, A.S., Babalola, O.O., 2021b. Unveiling the putative functional genes present in root-associated endophytic microbiome from maize plant using the shotgun approach. J. Appl. Genet. 62, 339–351.

Fadiji, A.E., Babalola, O.O., Santoyo, G., Perazzolli, M., 2022a. The potential role of microbial biostimulants in the amelioration of climate change-associated abiotic stresses on crops. Front. Microbiol. 12, 829099.

Fadiji, A.E., Santoyo, G., Yadav, A.N., Babalola, O.O., 2022b. Efforts toward overcoming drought stress in crops: revisiting the mechanisms employed by plant growth-promoting bacteria. Front. Microbiol. 13, 962427.

Fao 2016. Climate Is Changing. Food and Agriculture Must Too. Available online at: ⟨http://www.fao.org/3/I5758E/I5758E.pdf⟩ (accessed May 18, 2016).

Farooq, M., Hussain, M., Wahid, A., Siddique, K., 2012. Drought stress in plants: an overview. Plant Responses to Drought Stress. R. Aroca. Springer, Berlin, Heidelberg, Germany, pp. 1–33.

Farooq, M., Hussain, M., Wakeel, A., Siddique, K.H., 2015. Salt stress in maize: effects, resistance mechanisms, and management. A review. Agron. Sustain Dev. 35, 461–481.

Fernandez, C.W., Koide, R.T., 2013. The function of melanin in the ectomycorrhizal fungus *Cenococcum geophilum* under water stress. Fungal Ecol. 6, 479–486.

Fghire, R., Anaya, F., Ali, O.I., Benlhabib, O., Ragab, R., Wahbi, S., 2015. Physiological and photosynthetic response of quinoa to drought stress. Chil. J. Agric. Res. 75, 174–183.

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T., 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. Proc. Natl. Acad. Sci. U. S. A. 115, E1157–E1165.

Flemming, H.-C., Wingender, J., 2010. The biofilm matrix. Nat. Rev. Microbiol. 8, 623–633.

Forchetti, G., Masciarelli, O., Izaguirre, M.J., Alemano, S., Alvarez, D., Abdala, G., 2010. Endophytic bacteria improve seedling growth of sunflower under water stress, produce salicylic acid, and inhibit growth of pathogenic fungi. Curr. Microbiol. 61, 485–493.

Fuentes, A., Herrera, H., Charles, T.C., Arriagada, C., 2020. Fungal and bacterial microbiome associated with the rhizosphere of native plants from the Atacama Desert. Microorganisms 8, 209.

Furze, J.R., Martin, A.R., Nasielski, J., Thevathasan, N.V., Gordon, A.M., Isaac, M.E., 2017. Resistance and resilience of root fungal communities to water limitation in a temperate agroecosystem. Ecol. Evol. 7, 3443–3454.

Gao, C., Montoya, L., Xu, L., Madera, M., Hollingsworth, J., Purdom, E., Singan, V., Vogel, J., Hutmacher, R.B., Dahlberg, J.A., 2020. Fungal community assembly in drought-stressed sorghum shows stochasticity, selection, and universal ecological dynamics. Nat. Commun. 11, 1–14.

Garcia De Salamone, I., Döbereiner, J., Urquiaga, S., Boddey, R., 1996. Biological nitrogen fixation in Azospirillum strain-maize genotype associations as evaluated by the 15N isotope dilution technique. Biol. Fertil. Soils 23, 249–256.

Gavelienė, V., Jurkonienė, S., Jankovska-Bortkevič, E., Švegždienė, D., 2022. Effects of elevated temperature on root system development of two lupine species. Plants 11, 192.

Given, C., Häikiö, E., Kumar, M., Nissinen, R., 2020. Tissue-specific dynamics in the endophytic bacterial communities in arctic pioneer plant Oxyria digyna. Front. Plant Sci. 11, 561.

Glick, B.R., 2014. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol. Res. 169, 30–39.

Goda, H., Sasaki, E., Akiyama, K., Maruyama-Nakashita, A., Nakabayashi, K., Li, W., Ogawa, M., Yamauchi, Y., Preston, J., Aoki, K., 2008. The AtGenExpress hormone and chemical treatment data set: experimental design, data evaluation, model data analysis and data access. Plant J. 55, 526–542.

Groen, S.C., Joly-Lopez, Z., Platts, A.E., Natividad, M., Fresquez, Z., Mauck Iii, W.M., Quintana, M.R., Cabral, C.L.U., Torres, R.O., Satija, R., 2022. Evolutionary systems biology reveals patterns of rice adaptation to drought-prone agro-ecosystems. Plant Cell 34, 759–783.

Gull, A., Lone, A.A. & Wani, N.I. 2019. Biotic and abiotic stresses in plants. In abiotic and biotic stress in plants; De Oliveira, A.B., Ed.; IntechOpen: London, UK, 2019.

Gupta, A., Rico-Medina, A., Caño-Delgado, A.I., 2020. The physiology of plant responses to drought. *Science*368 266–269.

Han, Q.-Q., Lü, X.-P., Bai, J.-P., Qiao, Y., Paré, P.W., Wang, S.-M., Zhang, J.-L., Wu, Y.-N., Pang, X.-P., Xu, W.-B., 2014. Beneficial soil bacterium *Bacillus subtilis* (GB03) augments salt tolerance of white clover. Front. Plant Sci. 5, 525.

Harbort, C.J., Hashimoto, M., Inoue, H., Schulze-Lefert, P., 2020. A gnotobiotic growth assay for Arabidopsis root microbiota reconstitution under iron limitation. STAR Protoc. 1, 100226.

Hou, S., Thiergart, T., Vannier, N., Mesny, F., Ziegler, J., Pickel, B., Hacquard, S., 2021a. A microbiota–root–shoot circuit favours Arabidopsis growth over defence under suboptimal light. Nat. Plants 7, 1078–1092.

Hou, S., Wolinska, K.W., Hacquard, S., 2021b. Microbiota-root-shoot-environment axis and stress tolerance in plants. Curr. Opin. Plant Biol. 62, 102028.

Hussain, S., Khaliq, A., Ali, B., Hussain, H.A., Qadir, T., Hussain, S., 2019. Temperature extremes: impact on rice growth and development. In: In Plant Abiotic Stress Tolerance, 2019. Springer, Cham, Switzerland, pp. 153–171.

Inbaraj, M.P., 2021. Plant-microbe interactions in alleviating abiotic stress—a mini review. Front. Agron. 3, 667903.

Islam, F., Yasmeen, T., Arif, M.S., Ali, S., Ali, B., Hameed, S., Zhou, W., 2016. Plant growth promoting bacteria confer salt tolerance in Vigna radiata by up-regulating antioxidant defense and biological soil fertility. Plant Growth Regul. 80, 23–36.

Ismail, M.A., Amin, M.A., Eid, A.M., Hassan, S.E.-D., Mahgoub, H.A., Lashin, I., Abdelwahab, A.T., Azab, E., Gobouri, A.A., Elkelish, A., 2021. Comparative study between exogenously applied plant growth hormones versus metabolites of microbial endophytes as plant growth-promoting for *Phaseolus vulgaris* L. Cells 10, 1059.

Ito, O., O'toole, J.C. & Hardy, B. 1999. Genetic improvement of rice for water-limited environments. International Rice Research Institute, Los Banos, Philippines.

Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. Nat. Rev. Microbiol. 18, 35–46.

Javaid, M.M., Florentine, S., Mahmood, A., Wasaya, A., Javed, T., Sattar, A., Sarwar, N., Kalaji, H.M., Ahmad, H.B., Worbel, J., 2022. Interactive effect of elevated CO_2 and drought on physiological traits of *Datura stramonium*. Front. Plant Sci. 13, 929378.

Javed, T., Shabbir, R., Ali, A., Afzal, I., Zaheer, U., Gao, S.-J., 2020. Transcription factors in plant stress responses: challenges and potential for sugarcane improvement. Plants 9, 491.

Javed, T., Shabbir, R., Hussain, S., Naseer, M.A., Ejaz, I., Ali, M.M., Ahmar, S., Yousef, A. F., 2022. Nanotechnology for endorsing abiotic stresses: a review on the role of nanoparticles and nanocompositions. Funct. Plant Biol. https://doi.org/10.1071/FP22092.

Jez, J.M., Lee, S.G., Sherp, A.M., 2016. The next green movement: plant biology for the environment and sustainability. Science 353, 1241–1244.

Joo, G.-J., Kim, Y.-M., Kim, J.-T., Rhee, I.-K., Kim, J.-H., Lee, I.-J., 2005. Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. J. Microbiol. 43, 510–515.

Julkowska, M.M., Testerink, C., 2015. Tuning plant signaling and growth to survive salt. Trends Plant Sci. 20, 586–594.

Kandror, O., Deleon, A., Goldberg, A.L., 2002. Trehalose synthesis is induced upon exposure of Escherichia coli to cold and is essential for viability at low temperatures. Proc. Natl. Acad. Sci. U. S. A. 99, 9727–9732.

Kannojia, P., Sharma, P., Sharma, K., 2019. Climate change and soil dynamics: effects on soil microbes and fertility of soil. In: Choudhary, K.K., Kuma, A., Singh, A.K. (Eds.), Climate Change and Agricultural Ecosystems. Elsevier, Woodhead Publishing, Duxford, United Kingdom, pp. 43–64.

Karlowsky, S., Augusti, A., Ingrisch, J., Akanda, M.K.U., Bahn, M., Gleixner, G., 2018. Drought-induced accumulation of root exudates supports post-drought recovery of microbes in mountain grassland. Front. Plant Sci. 9, 1593.

Kasotia, A., Varma, A., Tuteja, N., Choudhary, D.K., 2016. Amelioration of soybean plant from saline-induced condition by exopolysaccharide producing Pseudomonas-mediated expression of high affinity K+-transporter (HKT1) gene. Curr. Sci. 1961–1967.

Khan, M.A., Asaf, S., Khan, A.L., Jan, R., Kang, S.-M., Kim, K.-M., Lee, I.-J., 2020a. Thermotolerance effect of plant growth-promoting *Bacillus cereus* SA1 on soybean during heat stress. BMC Microbiol 20, 1–14.

Khan, N., Bano, A., Ali, S., Babar, M.A., 2020b. Crosstalk amongst phytohormones from planta and PGPR under biotic and abiotic stresses. Plant Growth Regul. 90, 189–203.

Kul, R., Ekinci, M., Turan, M., Ors, S. & Yildirim, E. 2020. How abiotic stress conditions affects plant roots. In Plant Roots; Book and Demand: Norderstedt, Germany, pp 6–10.

Lemanceau, P., Blouin, M., Muller, D., Moënne-Loccoz, Y., 2017. Let the core microbiota be functional. Trends Plant Sci. 22, 583–595.

Lesk, C., Rowhani, P., Ramankutty, N., 2016. Influence of extreme weather disasters on global crop production. Nature 529, 84–87.

Li, H., La, S., Zhang, X., Gao, L., Tian, Y., 2021. Salt-induced recruitment of specific root-associated bacterial consortium capable of enhancing plant adaptability to salt stress. ISME J. 15, 2865–2882.

Liu, Y.-X., Qin, Y., Bai, Y., 2019. Reductionist synthetic community approaches in root microbiome research. Curr. Opin. Microbiol. 49, 97–102.

Lundberg, D.S., Ayutthaya, P.P.N., Straußß, A., Shirsekar, G., Lo, W.-S., Lahaye, T., Weigel, D., 2021. Host-associated microbe PCR (hamPCR) enables convenient measurement of both microbial load and community composition. Elife 10, e66186.

Ma, Y., 2019. Seed coating with beneficial microorganisms for precision agriculture. Biotechnol. Adv. 37, 107423.

Matsuda, Y., Noguchi, Y., Ito, S.-I., 2009. Ectomycorrhizal fungal community of naturally regenerated Pinus thunbergii seedlings in a coastal pine forest. J. For. Res. 14, 335–341.

Maya, M.A., Matsubara, Y.-I., 2013. Influence of arbuscular mycorrhiza on the growth and antioxidative activity in cyclamen under heat stress. Mycorrhiza 23, 381–390.

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G., Tognetti, V.B., Vandepoele, K., Gollery, M., Shulaev, V., Van Breusegem, F., 2011. ROS signaling: the new wave? Trends Plant Sci. 16, 300–309.

Mohamed, M.A., Ashraf, M.Y., Parvaiz, A., 2011. Evaluation of salicylic acid (SA) application on growth, osmotic solutes and antioxidant enzyme activities on broad bean seedlings grown under diluted seawater. Int. J. Plant Physiol. Biochem. 3, 253–264.

Morcillo, R.J., Manzanera, M., 2021. The effects of plant-associated bacterial exopolysaccharides on plant abiotic stress tolerance. Metabolites 11, 337.

Munir, N., Hanif, M., Abideen, Z., Sohail, M., El-Keblawy, A., Radicetti, E., Mancinelli, R., Haider, G., 2022. Mechanisms and strategies of plant microbiome interactions to mitigate abiotic stresses. Agronomy 12, 2069.

Muratova, A.Y., Turkovskaya, O., Antonyuk, L., Makarov, O., Pozdnyakova, L., Ignatov, V., 2005. Oil-oxidizing potential of associative rhizobacteria of the genus Azospirillum. Microbiology 74, 210–215.

Naseem, H., Bano, A., 2014. Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J. Plant Interact. 9, 689–701.

Naseem, H., Ahsan, M., Shahid, M.A., Khan, N., 2018. Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. J. Basic Microbiol 58, 1009–1022.

Naveed, M., Hussain, M.B., Zahir, Z.A., Mitter, B., Sessitsch, A., 2014. Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. Plant Growth Regul. 73, 121–131.

Naylor, D., Degraaf, S., Purdom, E., Coleman-Derr, D., 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. ISME J. 11, 2691–2704.

Nejat, N., Mantri, N., 2017. Plant immune system: crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. Curr. Issues Mol. Biol. 23, 1–16.

Nozoye, T., Nagasaka, S., Kobayashi, T., Takahashi, M., Sato, Y., Sato, Y., Uozumi, N., Nakanishi, H., Nishizawa, N.K., 2011. Phytosiderophore efflux transporters are crucial for iron acquisition in graminaceous plants. J. Biol. Chem. 286, 5446–5454.

Nunkaew, T., Kantachote, D., Nitoda, T., Kanzaki, H., Ritchie, R.J., 2015. Characterization of exopolymeric substances from selected Rhodopseudomonas palustris strains and their ability to adsorb sodium ions. Carbohydr. Polym. 115, 334–341.

Ochoa-Hueso, R., Collins, S.L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W.T., Sinsabaugh, R.L., Smith, M.D., Knapp, A.K., Power, S.A., 2018. Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. Glob. Chang Biol. 24, 2818–2827.

Omomowo, I.O., Fadiji, A.E., Omomowo, O.I., 2018. Assessment of bio-efficacy of *Glomus versiforme* and *Trichoderma harzianum* in inhibiting powdery mildew disease and enhancing the growth of cowpea. Ann. Agric. Sci. 63, 9–17.

Onwuka, B., Mang, B., 2018. Effects of soil temperature on some soil properties and plant growth. Adv. Plants Agric. Res. 8, 34–37.

Osman, K.T., 2018. Saline and Sodic Soils. Management of Soil Problems. Springer, Cham, pp. 255–298. https://doi.org/10.1007/978-3-319-75527-4_10.

Pan, C., Zhang, H., Ma, Q., Fan, F., Fu, R., Ahammed, G.J., Yu, J., Shi, K., 2019. Role of ethylene biosynthesis and signaling in elevated CO_2-induced heat stress response in tomato. Planta 250, 563–572.

Paterson, E., Sim, A., Davidson, J., Daniell, T.J., 2016. Arbuscular mycorrhizal hyphae promote priming of native soil organic matter mineralisation. Plant Soil 408, 243–254.

Pereira, A., 2016. Plant abiotic stress challenges from the changing environment. Front. Plant Sci. 7, 1123.

Preece, C., Peñuelas, J., 2016. Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. Plant Soil 409, 1–17.

Quiroga, G., Erice, G., Ding, L., Chaumont, F., Aroca, R., Ruiz-Lozano, J.M., 2019. The arbuscular mycorrhizal symbiosis regulates aquaporins activity and improves root cell water permeability in maize plants subjected to water stress. Plant, Cell Environ. 42, 2274–2290.

Rajasheker, G., Anil, K., Hima, K., Kavi, K., 2019. Bacterial cold shock proteins-the molecular chaperones for multiple stress tolerance. Adv. Biotechnol. Microbiol. 12, 555837.

Read, D., Bengough, A.G., Gregory, P.J., Crawford, J.W., Robinson, D., Scrimgeour, C., Young, I.M., Zhang, K., Zhang, X., 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. N. Phytol. 157, 315–326.

Roesti, D., Gaur, R., Johri, B., Imfeld, G., Sharma, S., Kawaljeet, K., Aragno, M., 2006. Plant growth stage, fertiliser management and bio-inoculation of arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria affect the rhizobacterial community structure in rain-fed wheat fields. Soil Biol. Biochem 38, 1111–1120.

Ruiz-Lozano, J.M., Aroca, R., Zamarre~No, A., Molina, S., Andreo-JimEnez, B., Porcel, R., Garcıa-Mina, J., Ruyter-Spira, C., LOpez-RAez, J., 2016. Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and improves drought tolerance in lettuce and tomato. Plant, Cell Environ. 39, 441–452.

Saijo, Y., Loo, E.P.I., 2020. Plant immunity in signal integration between biotic and abiotic stress responses. N. Phytol. t 225, 87–104.

Sánchez-Cañizares, C., Jorrín, B., Poole, P.S., Tkacz, A., 2017. Understanding the holobiont: the interdependence of plants and their microbiome. Curr. Opin. Microbiol. 38, 188–196.

Santos-Medellın, C., Liechty, Z., Edwards, J., Nguyen, B., Huang, B., Weimer, B., Sundaresan, V., 2021. Prolonged drought imparts lasting compositional changes to the rice root microbiome. Nat. Plants 7, 1065–1077.

Santos-Medellín, C., Edwards, J., Liechty, Z., Nguyen, B., Sundaresan, V., 2017. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. MBio 8, e00764–17.

Sardhara, K., Mehta, K., 2018. Effects of abiotic and biotic stress on the plant. Acad. J. Bot. Sci. 1, 15-9.

Sarkar, D., Rakshit, A., Parewa, H.P., Danish, S., Alfarraj, S., Datta, R., 2022. Bio-priming with compatible rhizospheric microbes enhances growth and micronutrient uptake of red cabbage. Land 11, 536.

Schimel, J.P., 2018. Life in dry soils: effects of drought on soil microbial communities and processes. Annu Rev. Ecol. Evol. Syst. 49, 409–432.

Shekhawat, K., Saad, M.M., Sheikh, A., Mariappan, K., Al-Mahmoudi, H., Abdulhakim, F., Eida, A.A., Jalal, R., Masmoudi, K., Hirt, H., 2021. Root endophyte induced plant thermotolerance by constitutive chromatin modification at heat stress memory gene loci. EMBO Rep. 22, e51049.

Shi, H., Shi, Q., Grodner, B., Lenz, J.S., Zipfel, W.R., Brito, I.L., De Vlaminck, I., 2020. Highly multiplexed spatial mapping of microbial communities. Nature 588, 676–681.

Shivaji, S., Prakash, J.S., 2010. How do bacteria sense and respond to low temperature? Arch. Microbiol. 192, 85–95.

Shrivastava, P., Kumar, R., 2015. Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. Saudi J. Biol. Sci. 22, 123–131.

Sieber, M., Pita, L., Weiland-Bräuer, N., Dirksen, P., Wang, J., Mortzfeld, B., Franzenburg, S., Schmitz, R.A., Baines, J.F., Fraune, S., 2019. Neutrality in the metaorganism. PLoS Biol. 17, e3000298.

Simmons, T., Styer, A.B., Pierroz, G., Gonçalves, A.P., Pasricha, R., Hazra, A.B., Bubner, P., Coleman-Derr, D., 2020. Drought drives spatial variation in the millet root microbiome. Front. Plant Sci. 11, 599.

Singh, K., 2016. Microbial and enzyme activities of saline and sodic soils. Land Degrad. Dev. 27, 706–718.

Singh, R.P., Shelke, G.M., Kumar, A., Jha, P.N., 2015. Biochemistry and genetics of ACC deaminase: a weapon to "stress ethylene" produced in plants. Front. Microbiol. 6, 937.

Singhal, R.K., Fahad, S., Kumar, P., Choyal, P., Javed, T., Jinger, D., Singh, P., Saha, D., Bose, B., Akash, H., 2022. Beneficial elements: New Players in improving nutrient use efficiency and abiotic stress tolerance. Plant Growth Regul. https://doi.org/10.1007/s10725-022-00843-8.

Song, F., Han, X., Zhu, X., Herbert, S.J., 2012. Response to water stress of soil enzymes and root exudates from drought and non-drought tolerant corn hybrids at different growth stages. Can. J. Soil Sci. 92, 501–507.

Spaepen, S., Vanderleyden, J., 2011. Auxin and plant-microbe interactions. Cold Spring Harb. Perspect. Biol. 3, a001438.

Sun, S., Li, S., Avera, B.N., Strahm, B.D., Badgley, B.D., 2017. Soil bacterial and fungal communities show distinct recovery patterns during forest ecosystem restoration. Appl. Environ. Microbiol. 83, e00966–17.

Talaat, N.B., Shawky, B.T., 2017. Microbe-mediated induced abiotic stress tolerance responses in plants. In: Singh, D.P., Singh, H.B., Prabha, R. (Eds.), Plant-Microbe Interactions in Agro-Ecological Perspectives. Springer, Singapore, pp. 101–133.

Thakuria, D., Talukdar, N., Goswami, C., Hazarika, S., Boro, R., Khan, M., 2004. Characterization and screening of bacteria from rhizosphere of rice grown in acidic soils of Assam. Curr. Sci. 86, 978–985.

Theocharis, A., Bordiec, S., Fernandez, O., Paquis, S., Dhondt-Cordelier, S., Baillieul, F., Clément, C., Barka, E.A., 2012. *Burkholderia phytofirmans* PsJN primes *Vitis vinifera* L. and confers a better tolerance to low nonfreezing temperatures. Mol. Plant Microbe Inter. 25, 241–249.

Tkacz, A., Bestion, E., Bo, Z., Hortala, M., Poole, P.S., 2020. Influence of plant fraction, soil, and plant species on microbiota: a multikingdom comparison. MBio 11, e02785–19.

Tocheva, E.I., Ortega, D.R., Jensen, G.J., 2016. Sporulation, bacterial cell envelopes and the origin of life. Nat. Rev. Microbiol. 14, 535–542.

Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., Singh, B.K., 2020. Plant–microbiome interactions: from community assembly to plant health. Nat. Rev. Microbiol. 18, 607–621.

Tsai, H.H., Schmidt, W., 2017. Mobilization of iron by plant-borne coumarins. Trends Plant Sci. 22, 538–548.

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., Dufresne, A., 2015. The importance of the microbiome of the plant holobiont. N. Phytol. 206, 1196–1206.

Vejan, P., Abdullah, R., Khadiran, T., Ismail, S., Nasrulhaq Boyce, 2016. Role of plant growth promoting rhizobacteria in agricultural sustainability—a review. Molecules 21, 573.

Velásquez, A.C., Castroverde, C.D.M., He, S.Y., 2018. Plant–pathogen warfare under changing climate conditions. Curr. Biol. 28, R619–R634.

Voges, M.J., Bai, Y., Schulze-Lefert, P., Sattely, E.S., 2019. Plant-derived coumarins shape the composition of an Arabidopsis synthetic root microbiome. Proc. Natl. Acad. Sci. U. S. A. 116, 12558–12565.

Wipf, H.M.-L., Bùi, T.-N., Coleman-Derr, D., 2021. Distinguishing between the impacts of heat and drought stress on the root microbiome of *Sorghum bicolor*. Phytobiomes J. 5, 166–176.

Worrich, A., Stryhanyuk, H., Musat, N., König, S., Banitz, T., Centler, F., Frank, K., Thullner, M., Harms, H., Richnow, H.-H., 2017. Mycelium-mediated transfer of water and nutrients stimulates bacterial activity in dry and oligotrophic environments. Nat. Commun. 8, 1–9.

Xu, L., Naylor, D., Dong, Z., Simmons, T., Pierroz, G., Hixson, K.K., Kim, Y.-M., Zink, E. M., Engbrecht, K.M., Wang, Y., 2018. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. Proc. Natl. Acad. Sci. U. S. A. 115, E4284–E4293.

Xu, L., Dong, Z., Chiniquy, D., Pierroz, G., Deng, S., Gao, C., Diamond, S., Simmons, T., Wipf, H.M.-L., Caddell, D., Varoquaux, N., Madera, M.A., Hutmacher, R., Deutschbauer, A., Dahlberg, J., Guerinot, M., Purdom, E., Banfield, J.F., Taylor, J. W., Lemaux, P., Coleman-Derr, D., 2021. Genome-resolved metagenomics reveals role of iron metabolism in drought-induced rhizosphere microbiome dynamics. Nat. Commun. 12, 3209.

Xu, Y., Zhang, G., Ding, H., Ci, D., Dai, L., Zhang, Z., 2020. Influence of salt stress on the rhizosphere soil bacterial community structure and growth performance of groundnut (*Arachis hypogaea* L.). Int. Microbiol. 23, 453–465.

Yadav, S., Modi, P., Dave, A., Vijapura, A., Patel, D. & Patel, M. 2020. Effect of abiotic stress on crops. In Sustainable Crop Production; IntechOpen: London, UK, 2020.

Yaish, M.W., Al-Lawati, A., Jana, G.A., Vishwas Patankar, H., Glick, B.R., 2016. Impact of soil salinity on the structure of the bacterial endophytic community identified from the roots of caliph medic (*Medicago truncatula*). PLoS One 11, e0159007.

Yang, Y., Guo, Y., 2018. Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol. 217, 523–539.

Yensen, N.P., 2008. Halophyte uses for the twenty-first century. In: Khan, M.A., Weber, D.J. (Eds.), Ecophysiology of high salinity tolerant plants, tasks for vegetation science. Springer, Netherlands, Dordrecht, The Netherlands, pp. 367–396.

Yoo, S.-D., Cho, Y., Sheen, J., 2009. Emerging connections in the ethylene signaling network. Trends Plant Sci. 14, 270–279.

Yooyongwech, S., Phaukinsang, N., Cha-Um, S., Supaibulwatana, K., 2013. Arbuscular mycorrhiza improved growth performance in Macadamia tetraphylla L. grown under water deficit stress involves soluble sugar and proline accumulation. Plant Growth Regul. 69, 285–293.

Zarattini, M., Farjad, M., Launay, A., Cannella, D., Soulié, M.-C., Bernacchia, G., Fagard, M., 2021. Every cloud has a silver lining: how abiotic stresses affect gene expression in plant-pathogen interactions. J. Exp. Bot. 72, 1020–1033.

Zarebanadkouki, M., Fink, T., Benard, P., Banfield, C.C., 2019. Mucilage facilitates nutrient diffusion in the drying rhizosphere. Vadose Zone J. 18, 1–13.

Zhang, H., Kim, M.-S., Sun, Y., Dowd, S.E., Shi, H., Paré, P.W., 2008. Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. Mol. Plant Microbe Inter. 21, 737–744.

Zhang, H., Zhu, J., Gong, Z., Zhu, J.-K., 2022. Abiotic stress responses in plants. Nat. Rev. Genet. 23, 104–119.

Zhang, Y., Gross, C.A., 2021. Cold shock response in bacteria. Annu. Rev. Genet. 55, 377–400.

Zhao, J., Lu, Z., Wang, L., Jin, B., 2020. Plant responses to heat stress: physiology, transcription, noncoding RNAs, and epigenetics. Int. J. Mol. Sci. 22, 117.