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Review Article

Beneficial Root-Associated Microbiome during Drought and Flooding Stress in Plants

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Abstract

Crop productivity is seriously threatened by the rise in the frequency and severity of drought and flood events around the world. Reduced drought and flooding stress in vulnerable species and ecosystems depends on our ability to comprehend how drought and flooding affect plant physiology and plant-associated microbes. Involvement of both abscisic acid ABA-dependent and ABA-independent pathways has been noted during drought. Hypoxic conditions impede hydraulic conductance, nutrient uptake and plant growth and development, as well as root aerobic respiration. The root microbiome, which works with the roots during drought and flood, is made up of plant growth-promoting rhizosphere, endophytes and mycorrhizas. A large number of phytohormones, primarily auxins, cytokinin and ethylene, as well as enzymes like 1-Aminocyclopropane-1-Carboxylate deaminase (ACC deaminase) and metabolites like exopolysaccharides are produced by rhizospheric microbes. These phytohormones, enzymes and metabolites have role in the induction of systemic drought tolerance in plants. Under hypoxia, anaerobic microbes with the potential to harm the plant due to their pathogenic behavior or soil denitrification ability are more likely to be present in the rhizosphere and roots. This review concentrates on the primary mechanisms of plant-microbe interactions under drought and flood stress as well as the importance of flood and drought-tolerant microbes in maintaining and increasing crop plant productivity under stress.

Key words: Endophyte, hypoxia, mycorrhiza, phytohormone, rhizobacteria, rhizosphere

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INTRODUCTION

Drought is a major stressor on most food crops, reducing crop yield. This stress is closely linked to the activity of Ribulose Bisphosphate Carboxylase Oxygenase (RuBisCo) and other photosynthetic enzymes, which occurs concurrently with an increase in reactive oxygen species (ROS) accumulation due to damage to the antioxidant enzyme machinery. This condition prevents seed formation and production[1]. Drought-resistant varieties, on the other hand, accumulate dissolved sugars, proline, glycine betaine, K^+ and other solutes, allowing physiological processes to continue normally[2,3]. The initial response to drought is mediated by hormonal signaling pathways regulated by abscisic acid (ABA) and jasmonic acid. When plants are stressed, ABA signals play an important role in closing stomata by inhibiting the entry of K^+ into guard cells, reducing transpiration rate[1].

Because it is environmentally friendly and inexpensive, microbiome application is widely used in drought stress management in plants. The rhizosphere is the soil fraction that is directly affected biochemically by root secretions and includes a layer of soil 1-5 mm from the root surface[4]. Rhizodeposition, during which roots exude dead cells, proteins, sugar and other substances, encourages the growth of a diverse microbiome, consisting of bacteria, archaea, fungi, viruses, oomycetes and their entire associated genomes. The root microbiome, which has long been recognized as an important component of plant health and resistance to environmental stress[1,5], contains a wide range of advantageous microbes, including mycorrhizal fungi, bacterial and fungal endophytes and Plant Growth-Promoting Rhizobacteria (PGPRs). Plant Growth-Promoting Rhizobacteria (PGPRs), bacterial and fungal endophytes and mycorrhizal fungi are among the beneficial microbes found in the root microbiome. All of these microbes play an important role in promoting plant growth, development and drought tolerance. Furthermore, these microbes contribute to the nutrient cycle by facilitating the uptake of N and P elements to support root architecture modification during drought, which is influenced by the secretion of phytohormones indole acetic acid (IAA), gibberellic acid (GA) and cytokinin[6-8].

Flooding is a natural disaster that threatens terrestrial ecosystems, which include production forests, natural forests and agricultural areas. Plants can adapt to natural flood conditions morphologically, anatomically, physiologically, metabolically and phenologically. However, the risk of flooding is increasing as a result of global climate change, hydrological disruption and land use changes, so efforts are being made to protect vulnerable forests and agricultural ecosystems from flooding and to increase plant tolerance to flooding[5].

Traditional water management infrastructure (such as drainage and dikes) and nature-based solutions are two basic strategies that can be implemented to alleviate flooding stress. Nature-based solutions use living organisms and/or landscape features to mitigate the effects of climate change. The plant-associated microbiome, which inhabits the external and internal spaces of plants, is susceptible to repeated waterlogging and submergence. Plants' ability to change is supported by the short generation time and high mutation and recombination rates of microorganisms[9]. Flooding stress can modify plant metabolism, morphophysiology and chemistry, which can change the microbiome's composition and functional characteristics both directly and indirectly[10]. However, it is the microbiome that can reduce stress by adapting to or tolerating new stressful conditions and metabolizing stress-induced signals. Flooding's impact on microbial diversity, the level of plant reaction and acclimation to flooding mediated by the microbiome and the potential for innovative use of plant microbiomes in dealing with flooding all require additional research by Martínez-Arias *et al.*[5].

This review focused on the effects of drought and flooding on plant physiology, as well as rhizosphere and root microorganisms. The importance of considering the microbiome in studies of plant adaptation and resilience to drought and flooding events is emphasized because of its critical role in drought and flood stress resilience.

Search method: The literature review was conducted online using the keywords "root microbes", "drought", "flood", "stress physiology" and "plant-microbe's interaction" on the Google Scholar and Science Direct websites. The review took place between February and June, 2023. The review yielded 1325 articles in total, but only 35 were chosen for this study. The titles, abstracts and text of the articles were reviewed independently by the authors.

EFFECTS OF DROUGHT ON PLANT PHYSIOLOGY

All plants respond to drought stress in roughly the same way, but the used specific strategy determines their level of resistance or susceptibility. The primary visible symptoms of a lack of water in plants are wilting and senescence. Several key physiological parameters as plant responses to drought included root development, stomatal closure, photosynthesis, ROS scavenging and ABA and jasmonic acid (JA) accumulation[11]. Coordination of stomatal closure, wilting point and stem hydraulic conductivity can reduce drought-induced injury by regulating water loss according to water availability[12]. When K^+ was applied exogenously in high doses, low K^+ sensitive cultivars showed increased accumulation of proline, antioxidant enzymes and photosystem II efficiency[13]. Roots stressed by drought have a higher accumulation of sugars, amino acids, lipids and antioxidants, implying that roots are the epicenter of plant responses to this stress[14]. During drought, changes in root architecture determine optimal soil water utilization and root development is determined by the coordinated effects of phytohormones such as brassinosteroids, ethylene and auxin, while, ABA and cytokinins play a role in the regulatory process[1]. The K^+, glycine betaine and proline contributed to leaf osmotic adjustment at the whole plant level, while Na^+ and proline contributed to leaf osmotic adjustment at the tissue level in wheat under water deficit[3]. Other plant physiological responses to drought included increased root growth and decreased seed germination, early growth, relative water content and chlorophyll content in finger millet varieties[15], decreased total chlorophyll and chlorophyll content in the leaves of North Sulawesi local rice as a response to PEG 8000-induced water deficit at the whole plant level[16] and decreased leaf relative water content in North Sulawesi local rice under polyethylene glycol (PEG) 8000-induced water deficit in at the tissue level[17]. The formation of a rhizosheath (a layer of soil that remains firmly attached to the root system) is determined by the type of roots and associated microbes. Under moderate drought conditions, rhizosheath formation increases due to the activity of 1-aminocyclopropane-1-carboxylate (ACC) degrading bacteria as a tolerance strategy[18].

Drought response in plants is controlled by ABA-dependent and ABA-independent signaling pathways. Drought responses in plants are controlled by ABA-dependent signaling pathways, which include reduction in water loss, protection against cellular dehydration, drought avoidance and drought tolerance. The ABA is a key metabolite that controls stomatal movement, early flowering, seed set, osmotic adjustment and other processes. To induce target genes for drought tolerance, ABA interacts directly or indirectly with transcription factors such as DREB (Dehydration-Responsive Element Binding), bZIP (Basic Leucine Zipper Domain), ABREs (ABA-responsive elements) and DREs (drought regulatory elements). Plant responses to drought regulated through ABA-independent signaling pathways include drought avoidance, regulation of flowering time, expression of drought-responsive genes, reduction of water loss, an increase of water uptake and an increase of root biomass and water uptake. A number of phytohormones besides ABA, including auxin, cytokinin, ethylene, jasmonic acid, salicylic acid and brassinosteroids, regulate an ABA-independent pathway[1].

EFFECTS OF FLOOD ON PLANT PHYSIOLOGY

Flooding is a common natural disaster that can submerge rice fields decrease agricultural yields and infrastructure damage. In addition, depending on the frequency and severity of floods, this abiotic stress can affect how successfully crops are harvested[19]. Floods affect plant metabolism differently depending on the species, origin and genotypes, as well as flood timing and duration. These metabolic changes impact the physiology and anatomy of plant organs, as well as the overall plant performance. Poor soil aeration due to flooding primarily affects root energy metabolism. The reduced respiration rate promotes glycolysis as part of a comprehensive reorganization of energy, carbon (C) and nitrogen (N) metabolism. Plants downregulate the ATP-consuming pathway to favor the regeneration of Nicotinamide Adenine Dinucleotide (NAD^+) for use in glycolysis as a strategy to acclimate to low O_2 levels. As a result, toxic ethanol accumulates more quickly in flood-intolerant species than in flood-tolerant ones. When hypoxia restricts mineral assimilation and absorption, an energy crisis results in root death and decreased water uptake and transport in living roots. In both root and aerial tissues, flooded plants have deficiencies in macro and micronutrient minerals, which further inhibit growth due to hormonal imbalance and insufficient energy[5].

Flooding also inhibits the formation and extension of lateral roots because ethylene, a gaseous phytohormone that accumulates in flooded plants, interferes with auxin local signaling[20]. Ethylene is synthesized in the shoots as a result of the oxidation of 1-Aminocyclopropane-1-Carboxylate (ACC) from the roots. This hormone, however, is produced by microbes associated with roots and plants and transported up to shoots from roots and soil. Thus hydraulic and chemical signals quickly propagate changes in root function to aerial components. The capacity of the xylem for water transport can be compromised early in a flood or later after a flood stress, due to decreased aquaporin activity during hypoxia and apoplastic water movement. Hypoxia causes apoplastic water movement and decreased aquaporin activity. Low xylem hydraulic conductance promotes gas movement in the xylem ducts while decreasing dissolved gibberellin and cytokinin transport to the shoot. Indeed, plant hormone synthesis and regulation (such as cytokinins, ABA and ethylene) are increasingly being considered from a holobiont perspective. Ethylene signaling is a plant-microbe interaction paradigm under stress. Hydraulic or chemical signals cause stomatal closure, which contributes to decreased leaf growth of flooded plants. Stomatal closure occurs frequently in flooded plants and the concentration of ABA in the leaves may not change or may even rise when the stomata are closed[5].

Another typical reaction of plants to flooding is a decrease in photosynthesis. Stomata closure reduces net CO_2 uptake and CO_2 diffusion to chloroplasts. Alternative energy dissipation mechanisms, such as heat exchange and photorespiration, are triggered by the limited amount of reducing power and energy used to reduce CO_2, but they are unable to stop permanent photo inhibition, chlorophyll degradation and leaf shedding. Because the available light to submerged plants is reduced and diffusion restrictions are spread across all gases, photosynthetic restrictions appear to be more rapid and greater when the plant is completely submerged. In flooded plants, a lack of N element uptake and assimilation can also limit photosynthetic capacity. The concentration of non-structural carbohydrates in both submerged and non-submerged organs of flooded plants is frequently higher than in non-flooded plants[21,22]. This increase in non-structural carbohydrates in leaves is also linked to phloem transport. Flood stress also causes dramatic changes in C and N metabolism and can alter metabolite partitioning inside and outside the plant, e.g., via root exudates[5].

Most terrestrial plants are unable to withstand prolonged flood stress. The accumulation of toxic compounds, C deficiency, cytoplasmic acidification, or disease can kill plants exposed to continuous or repeated flooding. The earlier the plant experiences stress, the more sensitive the species or genotype will be. Species that live in wetlands change adaptively to reduce the physiological stress of flooding. Herbaceous plants that are semi-aquatic, like rice, can alternate between a dormant metabolism that uses energy to conserve itself while submerged and an active metabolism that uses energy to emerge from a flood state[23,24]. The ability to minimize C use while maximizing C gain determines the amount of C that can be allocated to maintain hypoxic organs, which is a determining factor in surviving and recovering from the flood. As a result, the ability to control O_2 concentration is critical for maintaining respiration and photosynthesis[5].

The main physiological changes experienced by plants during flood stress are summarized below. The main and direct effect of flooding is reduced oxygen supply. Poor soil aeration alters root energy metabolism by inhibiting the TCA (tricarboxylic acid) cycle or Krebs cycle in mitochondria while stimulating glycolysis and fermentation, resulting in toxic ethanol accumulation in roots. Hypoxia also inhibits aquaporin activity, which, along with altered root metabolism, contributes to the cessation of lateral root formation and elongation. Changes in root function are quickly followed by changes in aerial plant parts, with hydraulic and chemical signals both contributing to root communication with shoots. Reduced xylem conductivity is caused by low aquaporin activity and increased apoplastic resistance to water movement. This process occurs concurrently with ABA accumulation in the leaves, causing the stomata to close. Closing stomata reduces CO_2 uptake, hampered photosynthesis and reduces carbohydrate production. Furthermore, leaf chlorophyll concentrations, such as chlorophyll a, b and total, decreased in North Sulawesi rice varieties during the vegetative stage because of photoinhibition and decreased root nitrogen uptake. Under hypoxic conditions, ethylene is rapidly synthesized in roots or leaves from its precursor ACC. Ethylene accumulation also leads to the formation of aerenchyma, which is a network of numerous suberin hypertrophied lenticels, adventitious roots and pneumatophores. Aerenchyma development promotes gas diffusion while the formation of a network rich in suberin prevents radial O_2 loss or ROL. Oxygen transport to submerged plant parts is enabled by the formation of hypertrophied lenticels, adventitious roots and pneumatophores[5,25].

Various changes that occur in host plants when flooded such as anatomy, allocation and metabolism of C and N, gas concentrations, sap pH, etc., can have an impact on the microbiome by the food supply and the physicochemical microenvironment. On the other hand, the microbiota, or the relative abundance or sensitivity to the stress of certain taxa, can also have an impact on a plant's ability to adapt its metabolism, physiology and anatomy to floods (flood tolerance) and the capacity of microbes to recolonize in plants or the rhizosphere depends on changes in the composition of the microbial community that are induced by floods depends on changes in the composition of the microbial community that are induced by floods[5,26].

EFFECTS OF DROUGHT ON RHIZOSPHERE MICROORGANISMS

The plant rhizosphere (the area around plant roots) serves as a concentrated reservoir for both beneficial and harmful soil microflora. Plant roots and microorganisms interact in two ways to regulate growth, development and health. However, the association between various soil microbes and rhizospheric regions is highly plant-specific. Soil type, pH, humidity, nutrient conditions and climate all have an impact on this association[27]. These conditions demonstrate the rhizobiota's highly diverse characteristics as well as their dynamic ability to change under stressfull conditions. Several studies have shown that rhizosphere microbial populations change in response to drought, temperature, CO_2 and other stressors. Most plants' acclimatization to stressfull conditions is aided by an increase in microbial population. Under stress conditions, root exudates have a strong influence on the microbial rhizospheric community and root microbiome analysis can reveal ecosystem function. As a result, microbiome exploration is being conducted in order to identify new microbial populations that may be beneficial for increasing plant growth and development in response to climate change[1].

The root microbiome diversity of rice plants grown in various soil conditions is being investigated. Drought, regardless of soil type or cultivar, alters microflora populations by promoting the growth of drought-resistant actinobacteria and chloroflexi while suppressing acidobacteria and deltaproteobacteria populations. Drought-induced changes in the root microbiome aid plant adaptation to stress[28]. Among the 22 *Bacillus* spp., strains isolated from the rhizosphere of Guinea grass (*Megathyrsus maximus*), bacteria *B. amyloliquefaciens*, *B. aryabhattai* and *B. licheniformis* are the most drought-tolerant and can improve plant resistance[29]. Other bacterial strains isolated from gum arabic (*Acacia arabica*), such as *Bacillus*, *Enterobacter*, *Moraxella* and *Pseudomonas*, increased plant resistance to drought, as evidenced by an increase in the number of tillers and wheat spikelets[30]. Changes in the abundance of rhizosphere microflora are strongly influenced by groundwater status (irrigated versus non-irrigated), which appears to control rhizosphere physiological processes. Reducing CO_2 emissions and H_2 levels in water-stressed wheat rhizospheres reduced bacterial populations but not fungal populations, which were more resistant to changes in water concentration. Furthermore, endophytic microbial colonization in roots demonstrates the ability to overcome low water availability[27].

The composition of the rhizomicrobiome depends on root architecture and the increase in the number of specific bacterial strains in the soil. The plant growth and root plasticity of *Arabidopsis thaliana* improved after *Sphingomonas* sp., was added to the rhizosphere, resulting in changes to the pre-existing microbial population[31]. During drought stress, *Sphingomonas* inoculation resulted in the abundance of Betaproteobacteria, Burkholderiaceae and Rhizobiaceae during drought stress. *Microbacterium*, *Arthrobacter koreensis* and *Rhodococcus* sp., are the most tolerant genus and this is related to the level of trehalose production during drought treatment[32]. These microbes produce IAA, GA, SA, ABA, ACC deaminase and antioxidant enzymes. The presence of microbially-produced growth regulators and microbial drought tolerance play a role in improving plant drought tolerance and contribute to better survival in plants inoculated during drought. Phytohormones and exopolysaccharide secreted by the bacteria *Pseudomonas aeruginosa*, *Bacillus endophyticus* and *Bacillus tequilensis* play a role in *Arabidopsis* seedling tolerance to osmotic stress[33].

EFFECTS OF FLOOD ON RHIZOSPHERE MICROORGANISMS

The rhizosphere is the soil fraction influenced biochemically by plant roots, specifically, the soil layer is 1-5 mm from the root surface[26]. The microbiota of the rhizosphere which consists of bacteria, archaea, fungi, viruses and oomycetes, as well as the genomes linked to those microbiomes, compose the community of rhizospheric microbes. The release of mucilage, hormones and other compounds from roots influences microbial growth, attracts certain microbes and can alter rhizosphere components[34]. Plants specifically recruit several beneficial microbes to increase stress tolerance. As a result, changes in the rhizosphere microbiome can impact plant performance. Many studies on the effect of flooding on the rhizosphere microbiome have been conducted on herbaceous plants, particularly paddy rice, which is economically valuable, whereas studies on woody species are still rare. Most studies focus on the effects of flooding on bacteria, but there are few studies on the effects of flooding on fungi, archaea, oomycetes and viruses. During flooding, the microbial community in bulk and rhizosphere soil changes. Because bulk soil is the primary source of microorganisms recruited by plant roots into the rhizosphere, flooding's effect on the microbial composition of bulk soil can also affect the rhizosphere's composition[5].

The direct effect of flooding on rhizosphere soil microbiota is caused by a gradual decrease in O_2 as water is absorbed into soil pores. As soil becomes anoxic and loses oxygen, the microbial composition changes, causing a transition from a predominance of aerobic organisms to more facultative anaerobes and then strict anaerobes. The microbial composition changes as soil goes from being oxygenated to being anoxic, causing a shift from a predominance of aerobic organisms to more facultative anaerobes and then to strict anaerobes. Flooding causes a dramatic increase in the composition of rhizosphere microbiota. Plant-detrimental taxa (such as *Clostridium* or *Geobacter*) increase the proportion of bacteria that can respire anaerobically (Phylum Firmicutes and Desulfobacterota), while Actinobacteria and Proteobacteria (especially the (the families Rhizobiaceae and Xanthobacteraceae) as well as plant-friendly bacterial taxa (like those from the genera *Streptomyces* and *Sphingomonas*) decline[35]. Some microbes produce osmoprotectants or endospores to withstand flood stress, switching their metabolism to anaerobic respiration, fermentation or microaerophily[5]. However, more research is required to determine how flooding interacts with other factors to regulate microbial composition in the rhizosphere. Flood duration, drainage conditions, pH, redox status and C dynamics all have the potential to change the structure and composition of the rhizosphere microbiota. Furthermore, the composition of rhizosphere bacteria is influenced by host species- and genotype-specific traits, thus, the effect of flooding on the rhizosphere microbiota is highly dependent on specific host traits.

Flood-induced stress in the plants themselves can have an indirect effect on the rhizosphere microbiota. Stress, for example, can alter the quantity and quality of root exudates, altering the biochemical composition of the rhizosphere and the metabolism of heterotrophic bacteria. Specific plant adaptations to facilitate O_2 transport (e.g. aerenchyma) can mitigate changes in the rhizosphere and soil microbes. Stress on plants can alter the composition of root exudates, resulting in dysbiosis (a microbial population imbalance) in the rhizosphere. The presence of specific microbial groups, such as PGPR (plant growth promoting rhizobacteria), which cut chemical bonds in the ethylene precursor ACC (1-Aminocyclopropane-1-Carboxylate) by releasing ACC-deaminase, can reduce stress on plants and indirectly on microbes[36].

Compounds released by the roots during the rhizodeposition process (for example, exudates, border cells, or mucilage) account for 25% of the element C allocated to underground plant parts and provide approximately 17% of the element C fixed in photosynthesis. Changes in rhizosphere C input cause a rhizosphere priming effect, in which new soil C stimulates the decomposition of old soil C. The mechanism underlying the rhizosphere priming effect is unknown, possibly because the flow of C and N in the rhizosphere is complex and highly dependent on plant and environmental factors[5,37]. Here are some explanations for the rhizosphere priming effect:

- When N availability in the rhizosphere is limited, microbes use the C provided by assimilable compounds to synthesize hydrolyzed enzymes and then more organic material to obtain additional N
- The C:N ratio is more important than the C input itself for the rhizosphere priming effect, although, abiotic stress alters the composition and quantity of root exudate, it is unknown how flood stress affects the total organic C excreted by roots
- Because soil anoxia reduces net photosynthesis, the amount of root-derived C in the rhizosphere is limited after flooding

The amount of root-derived C during flooding is largely determined by factors that affect the degree of reduction in photosynthesis rate (such as host-specific properties or flooding duration). Changes in C input to soil appear to have a greater impact on microbial function than on overall microbial diversity. Plant roots can release specific phytotoxic compounds such as ethanol, acetaldehyde and cyanogenic compounds during anoxic conditions to repair cell damage caused by flooding and some of these compounds affect the rhizosphere microbiome. The release of ethanol, for example, acts as a chemical attractant for various root pathogens such as *Phytophthora* sp. and *Fusarium* sp.[5,37].

Flooding alters the microbial composition of the rhizosphere and bulk soil by shifting the dominance of aerobic microorganisms to anaerobic microorganisms. The continuous movement of microbes from the bulk soil to the rhizosphere can have an impact on the rhizosphere's taxonomic composition. The variation in the soil's nutrient status is one of the most significant effects of changes in the soil microbiome caused by flooding. Nitrifying microorganisms are inhibited and denitrifiers increase as a result. Nitrates (NO^{3-}) and Nitrites (NO^{2-}) are consumed to produce various gaseous nitrogen compounds (NO, N_2O and N_2). The N deficiency can have a significant impact on many aspects of plant growth. Because of the degradation of soil organic compounds by anaerobic methanogenic microbes, hypoxic conditions in bulk soil induce methanogenic processes. This process produces Methane (CH_4) and CO_2, which can be released into the atmosphere through soil or plant tissue[5].

In flooded soils, plants and soil microbes compete for O_2. Wetland plants that adapt to anoxic conditions form aerenchyma, which transports O_2 from aerial tissues to the roots (while CO_2, ethylene and methane are transported from the soil to the canopy and atmosphere). The oxygen transported in this manner reaches the root cells, but it is also partially released into the rhizosphere about 1-3 mm from the root surface via a process known as radial O_2 loss (ROL). The microorganisms of bulk soil can endure anaerobic conditions. Aerobic bacteria in the rhizosphere, including heterotrophic bacteria, methane-oxidizing bacteria and autotrophic bacteria involved in ammonium nitrification into nitrate, are made more active by input O_2[38,39], while anaerobic processes like denitrification, N_2 fixation and methanogenesis take place mostly in bulk soil[40]. Under well-watered soil conditions, some species, such as maize, wheat and barley, do not form aerenchyma, however, aerenchyma formation is induced during flooding and aids in the recovery of aerobic microbial processes in the rhizosphere.

Flooding's impact on rhizosphere microorganisms can have an impact on soil nutrition, particularly in terms of N availability. Low O_2 concentrations in the rhizosphere can inhibit the aerobic metabolism of autotrophic bacteria responsible for nitrification, which occurs concurrently with plant uptake of Nitrate (NO^{3-}), resulting in progressive NO^{3-} loss from the soil. Under anoxic conditions, heterotrophic facultative anaerobic bacteria use NO^{3-} and NO^{2-} as terminal acceptors of electrons, resulting in the release of some gases such as nitric oxide (NO), Nitrous Oxide (N_2O) and dinitrogen (N_2) to the soil. These gases undergo significant denitrification, which can result in N loss from the soil. Limited N availability as a result of denitrification can affect the growth, leaf area, photosynthesis rate and leaf tenacity in plants[40,41].

Some members of the rhizosphere microbiota may improve plant tolerance to flooding or waterlogging. Plant Growth Promoting Rhizobacteria (PGPR) are the most beneficial rhizosphere microorganisms, increasing plant growth and resilience to various abiotic stressors[42,43]. Specific PGPR reduces the amount of ethylene that accumulates in plants when they are flooded, reducing the negative effects of high ethylene content on plant growth and development. In the rhizosphere or the root endosphere, PGPR produces ACC deaminase, an enzyme that can break the bonds of ACC (ethylene precursor in plants), limiting the amount of ethylene that accumulates in plant tissues. As a result, artificial selection and inoculation of PGPR are required to improve plant performance against various stressors such as flooding, salinity, heavy metals, or drought. Several PGPRs, including *Bacillus*, *Microbacterium*, *Methylophaga* and *Paenibacillus*, have been artificially applied to rice crops and have proven to be beneficial in dealing with floods by lowering ethylene levels[44]. Several PGPRs from the genera *Achromobacter*, *Serratia*, *Herbaspirillum* and *Ochrobactrum* have the potential to protect waterlogged *Ocimum* plants from flood stress[45]. *Pseudomonas putida* can overcome the hypoxic (hypoxic) stress inhibitory effect on cucumber plant biomass[46]. The formation of ROL barriers by soil anaerobic microbes is another example of flood tolerance induction. The selection of organic acids (acetic, propionic, butyric and hexanoic acids) by anaerobic microbes appears to stimulate this effect during organic matter decomposition in the soil[47].

EFFECTS OF DROUGHT ON ROOT MICROORGANISMS

Plant Growth-Promoting Rhizobacteria (PGPR): The PGPR refers to a group of bacteria that live near the root surface or more specifically, in the rhizosphere. These PGPR strains can produce IAA, solubilize phosphate, have ACC deaminase activity and produce siderophores. The PGPR strains improve crop tolerance by increasing the accumulation of compatible solutes like proline and glycine betaine, producing secondary metabolites and inducing the expression of many plant-specific genes. Exploration of PGPR populations in plants under stress conditions recently demonstrated the adaptability of these microorganisms to translate induced systemic tolerance (IST)[48] (Table 1). The application of PGPR can increase the biosynthesis of osmolytes and antioxidant enzymes in plants during drought. Drought mitigation was observed in wheat plants inoculated with *Klebsiella* spp., *Enterobacter ludwigii* and *Flavobacterium* sp. Wheat plants inoculated with PGPR strains also showed improved vegetative growth, higher relative water content (RWC), lower malondialdehyde (MDA) content and increased accumulation of proline and other stress-related metabolites[49] (Table 1).

Root endophytes: Endophytes are organisms found in plant tissues such as roots, shoots or leaves that have no negative impact on the host plant. Several bacterial and fungal endophytes contribute significantly to plant drought tolerance. Inoculated drought-stressed sorghum plants with root endophytic bacteria such as *Ochrobactrum* sp., *Microbacterium* sp., *Enterobacter* sp. and *Enterobacter cloacae* promote growth and osmotic adjustment. Inoculated plants accumulated more compatible solutes, such as proline, due to the upregulation of proline biosynthesis genes such as SbP5CS 1 and SbP5CS 2 (Pyrroline-5-Carboxylate Synthase genes)[50] (Table 1). Furthermore, there were three types of endophytic bacteria *Bacillus* isolated from upland rice varieties could mitigate the effects of drought on wheat plants[51]. During drought, the inoculated wheat plants showed an increase in RWC, antioxidant enzyme activity and sugar and proline accumulation (Table 1). Furthermore, inoculation of endophytic fungi, one of which is *Piriformospora indica*, plays a role in plant tolerance to drought. *Piriformospora indica* inoculated into drought-resistant barley revealed the expression of several genes that regulate the synthesis of stress signaling proteins, transporters, enzymes in important metabolic pathways, autophagy and up-regulation of proteins involved in plant protection against oxidative stress (Table 1)[52]. During drought stress, inoculation of *P. indica* on rice seedlings increases nutrient (Zn and P) uptake as well as growth and biomass (Table 1)[53].

Table 1: List of microbes attenuated drought stress in some crop plants

Microbes	Crop plants	References
PGPRs		
Pseudomonas putida strain FBKV2	*Zea mays* L.	Vurukonda *et al.*[48]
Klebsiella spp., *Enterobacter ludwigii* and *Flavobacterium* sp.	*Triticum* sp.	Gontia-Mishra *et al.*[49]
Bacillus cereus	*Sorghum bicolor* L. Moench	Saad and Abo-Koura[66]
Pseudomonas aeruginosa, *Enterobacter cloacae*, *Achromobacter xylosoxidans* and *Leclercia adecarboxylata*	*Zea mays* L.	Danish *et al.*[67]
Endophytes		
Piriformospora indica	*Oryza sativa* L. and *Hordeum vulgare* L.	Ghaffari *et al.*[52] and Saddique *et al.*[53]
Bacillus lentus, *Bacillus subtilis* and *Bacillus cereus*	*Oryza sativa* L.	Meenaksi *et al.*[51]
Ochrobactrum sp. strain EB-165, *Microbacterium* sp. strain EB-65, *Enterobacter* sp. strain EB-14 and *Enterobacter cloacae* strain EB-48	*Sorghum bicolor* (L.) Moench	Govindasamy *et al.*[50]
Arbuscular mycorrhizal fungi (AMF)		
Glomus mosseae	*Triticum* sp.	Bernando *et al.*[72]
Glomus versiforme	*Zea mays* L.	Begum *et al.*[54]
Funneliformis mosseae, Funneliformis geosporus, Claroideoglomus, claroideum, Glomus microaggregatum and *Rhizophagus irregularis*	*Oryza sativa* L.	Chareesri *et al.*[55]

Table 2: List of microbes dominated in soils subjected to flood of some crop plants

Microbes	Crop plants	References
Endophytes		
Deltaproteobacteria	*Oryza sativa* L.	Chialva *et al.*[56]
Phylum euryarchaeota	*Oryza sativa* L.	
Firmicutes	*Oryza sativa* L.	Ferrando and Scavino[57]
Aquaspirillum	*Populus*	Graff andConrad[58]
Cryptococcus, *Exophiala*, *Sporobolomyces* and *Rhodotorula*	*Camassia*	Freed *et al.*[59]
Arbuscular mycorrhizal fungi (AMF)		
Glomus intraradices and *Entrophospora colombiana*	*Phaseolus vulgaris*	Sah *et al.*[73]
Ectomycorrhizae (ECM)		
Laccaria spp. and *Thelephora terrestris*	*Pinus densiflora*	Cho *et al.*[60]
Cenococcum geophilum	*Quercus ilex*	Corcobado *et al.*[61]

Arbuscular mycorrhizal fungi (AMF): The AMF are highly specialized root endophytes that are found in a wide range of plants. AMF effectively protects plants against a variety of environmental stresses, as demonstrated by the examples below. Maize plants inoculated with AMF grew faster and had higher photosynthetic rates, more photosynthetic pigments and better nutrient uptake. Furthermore, there is an increase in the accumulation of compatible solutes that maintain plant water status[54] (Table 1). The AMF mediated drought tolerance in rice plants by increasing phosphate and IAA concentrations[55]. The proteome of several drought-prone wheat genotypes was significantly altered by AMF. Differential expression revealed that proteins involved in cell wall integrity and carbohydrate biosynthesis were upregulated, while other stress-related factors, such as enzymes involved in ethylene production, were downregulated (Table 1).

EFFECTS OF FLOOD ON ROOT MICROORGANISMS

Root endophytes: The decrease in endophytic colonization of flooded plants is proportional to the flood level and duration. This is due to the fact that some of the endophytes that colonize terrestrial plant roots are obligate aerobes and their survival is limited in hypoxic conditions[5]. Endophytes (fungi, bacteria, or groups of fungi that respire anaerobically) tend to proliferate during floods. Flooding, for example, increases the number of obligate anaerobic bacteria such as Deltaproteobacteria or Firmicutes in roots[56,57] (Table 2) and Proteobacteria groups such as the genus *Aquaspirillum* in the rhizoplane (external root layer) of flooded *Populus* roots[58] (Table 2). The number of anaerobic yeasts such as *Cryptococcus*, *Exophiala*, *Sporobolomyces* and *Rhodotorula* increases in hypoxic conditions[59] (Table 2). Methanobacteria (phylum euryarchaeota) proliferate in flooded rice roots under anaerobic conditions[56] (Table 2). Changes in the chemical composition of ecological niches caused by flooding can also result in the restructuring of microbial communities. Root endophytes can increase flood tolerance by influencing the development of specific anatomic structures like aerenchyma or ROL barriers. Endophytic microbe-induced improvements in plant physiology contribute to increased flood tolerance[5].

Mycorrhizal fungi: Flooding and waterlogging have recently been extensively studied in terms of their effects on the abundance and diversity of mycorrhizae. The inhibition of arbuscular mycorrhizae fungi (AMF) formation caused by flooding varies among mycorrhizal species and this influences hypoxia, which inhibits AMF spore germination and hyphal growth. Aerenchyma formation in the root cortex is associated with the presence of several AMF species in a flooded environment. This aerenchyma network, because it facilitates gas exchange, benefits plants as well as mycorrhizae and other aerobic microbes[5]. The AMF is more prevalent in frequently flooded soils. The AM and ectomycorrhizae (ECM) can be found in a variety of plant species, including *Populus* and *Salix*. Some ECM fungi thrive in permanently flooded conditions. *Laccaria* spp., *Thelephora terrestris*[60] (Table 2) and *Cenococcum geophilum*[61] (Table 2) are examples of flood-resistant. Seedlings grown in wet forests can be inoculated with flood-resistant mycorrhizal fungi. Association with flood-tolerant mycorrhiza can help improve plant vitality by reducing pathogen infection and assisting plant recovery from flooding and root rot.

APPLICATION OF DROUGHT-TOLERANT AND FLOOD-TOLERANT MICROORGANISMS: FUTURE PROSPECTS

Drought: The development of microbial-based biofertilizers makes it possible to harness, the potential of drought-tolerant microbes to increase plant resistance during drought in the field. This biofertilizer was created in response to calls to reduce the use of chemical fertilizers and pesticides in a sustainable agri-food system. The introduction of various chemical compounds into the environment usually alters the soil's physicochemical and biological balance. Biofertilizers will restore the soil to its natural state[62]. A good fertilizer formulation should include metabolically active microorganisms that have a longer life span while also being environmentally friendly and biodegradable[63]. Despite the fact that some microbes have the potential to improve crop production and health in adverse conditions, the development and commercialization of drought-tolerant microbial-based biofertilizers is still a long way off. Many efforts, however, have been made to develop biofertilizers that can assist plants in dealing with drought stress[1].

Plant Growth-Promoting Microbes (PGPM) are the most commonly used microbes as biofertilizers in comparison to other fungi and bacteria. The application of PGPM can have an effect on plant growth and appearance, either directly or indirectly. The direct mechanism works by producing specific compounds that can stimulate plant growth and increase nutrient availability and uptake (phosphate solubilization, siderophores or low-weight, high-affinity ion chelating molecules produced in response to iron deficiency, indole-3-acetate acid, nitrogen fixation). The indirect mechanism is carried out by suppressing plant pathogens. When exposed to nutritional and other abiotic stresses or when restoring contaminated soils, some Plant Growth-Promoting Rhizobacteria (PGPR) have beneficial effects on plant growth. Plants can also form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), which can increase root surface area for nutrient absorption[62].

Mycorrhizae in conjunction with *Azotobacter* and *Azospirillium* could be used as biofertilizers[64]. During drought stress, the use of these three types of microbes effectively increased root and shoot biomass, proline, carotenoid, essential oil, nitrogen and potassium content in *Valeriana officinalis*. The combination of *Glomus mosseae* and two PGPR strains (*Pseudomonas putida* and *Pantoea agglomerans*) as a biofertilizer increased leaf wet weight, chlorophyll content and photosynthetic rate in water-stressed *Aloe vera*[65]. The beneficial effects of PGPR strains in combination with other fertilizers have been studied. Pre-treatment of *Sorghum bicolor* seeds with *Bacillus cereus* and potassium silicate before sowing improved vegetative growth, relative water content, electrolyte leakage and osmotic potential in drought-stressed plants[66]. Furthermore, the *Bacillus cereus* and potassium silicate combination feeds the soil rhizosphere microflora. Application of a combination of PGPR strains that produce ACC deaminase (*Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Achromobacter xylosoxidans* and *Leclercia adecarboxylata*) and timber waste biochar significantly improves drought-tolerance ability in corn plants based on increased growth rate, production, gas exchange ratio and photosynthetic pigment concentration in plants experiencing drought stress and inoculated with this bioformulation[67]. Furthermore, the combination of PGPR and plant growth regulators improves chickpea plant drought tolerance. When drought caused an increase in chlorophyll content, sugar concentration, proline content and antioxidant enzyme activity, chickpea varieties sensitive to drought were given a combination of PGPR and growth regulator (SA and putrescine) treatment. This bioformulation also promotes the accumulation of various metabolites in chickpea leaves, including L-asparagine, glycerol, riboflavin, aspartate and 3-hydroxy-3methyglutarate[68]. The combination of arbuscular mycorrhizal fungi and biocharcoal reduced drought stress in chickpea plants by elevating biomass, photosynthetic efficiency and leaf water content and improved nitrogen fixation in stressed plants[69].

The ability of microbial inoculants to form colonies in external or internal plant tissues, interact well with the host and thrive in the soil alongside autochthonous microorganisms in a rhizocompetent manner determines their success as biofertilizers. In general, bacterial transfer, survival in the rhizosphere by competing with other microbes, attachment and colonization on the root surface (for example, by forming biofilms) and synergistic interactions with host plants all contribute to rhizosphere microbial colonization[62].

Flood: In contrast to the information on the role of microbes in plant tolerance to drought, little is known about the factors that affect long-term plant acclimation to flooding, as well as the ability of plants to survive and recover and the conditions of plant recolonization by symbionts. Flooded plants change their metabolism and physiological processes to adapt to hypoxia, which causes changes in microbial trophic interactions throughout the plant. Flooding stress signalling and tolerance in plants are mediated by a variety of endophytic and rhizospheric fungi and bacteria. However, the process by which physiological changes in plants cause changes in microbes is unknown. When compared to plant-microbe interactions during drought stress, nutrient stress, or plant disease, there is still a significant knowledge gap in understanding how flooding and waterlogging affect the microbiome below and above the soil, as well as the consequences of these conditions on plants[70,71]. The role of microbiome diversity and composition in flooding stress tolerance, as well as the direct and indirect effects of flooding on the microbiome, are still being investigated. Various manipulative experiments evaluating plant responses to flooding with and without symbionts can overcome the difficulty of distinguishing plant responses from symbiont-mediated stress responses. In this experiment, microbes must be isolated and their functional roles defined before inoculating plants with beneficial microbes to help them cope with stress. Observations on various plant species will aid in understanding the complex plant microbial network and the processes that occur during flooding stress. To show patterns of microbial diversity in different parts before and after the flood, more information about temporal changes in species- and plant part-specific microbial communities is required[20].

CONCLUSION

This review focuses on the main effects of drought and flood stress on plants, as well as the root microbiome undercurrents that aid in plant recovery from these stresses. Rhizospheric microbes are prolific producers of phytohormones, primarily auxins, cytokinin and ethylene, as well as enzymes such as ACC deaminase and metabolites such as exopolysaccharides, which aid in inducing systemic tolerance to drought. Plants that have been flooded alter their physiology and metabolism to adapt to hypoxia, which causes variations in microbial trophic interactions in various plant parts. On the other hand, some rhizospheric or endophytic bacteria and fungi may support plant flooding stress signaling and tolerance. Drought and flood-tolerant microbe isolation has advanced significantly, but there is still a vast ocean of microbial diversity yet to be explored. More research on the diversity of microbes that colonize the rhizosphere and the host plant microbial network during drought and flooding is required to assist plants in adapting to these stressors.

SIGNIFICANCE STATEMENT

This study found that the diversity of microbes that colonize the rhizosphere, as well as the main mechanisms of host plant and microbe interactions under drought and flood stress, are required to help plants adapt to these stresses. Drought and flood-tolerant microbes are critical for maintaining and improving crop plant productivity under these conditions. Although significant progress has been made in the isolation of drought and flood-tolerant microbes, there is still a vast ocean of microbial diversity to be explored. The findings of this study may point researchers in a new direction in their investigation of drought and flood-tolerant microbes.

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