Cross-Talk Between the Microorganisms and Genetic Drivers of Drought Stress Responses: Present Understanding and Prospects for Crop Improvement under Drought Environment

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Cross-Talk Between the Microorganisms and Genetic Drivers of Drought Stress Responses: Present Understanding and Prospects for Crop Improvement under Drought Environment

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A B S T R A C T

Long-lived plants, such as perennial woody species, are subjected to harsh environmental circumstances as a result of global warming. Drought stress is one of the most harmful abiotic stresses to plant growth and productivity of all the abiotic stresses. A group of microbes and microbe-derived substances that have been shown to improve plant development under biotic and abiotic stress conditions. Plants are home to a wide variety of microorganisms. Members of these microbial communities interact with one another and with the plant, and there is mounting evidence that the microbial community can help plants develop, enhance drought tolerance, aid disease defence, and even help with environmental remediation. These bacteria supply the plant with a variety of services and benefits in exchange for the plant providing decreased carbon and other metabolites to the microbial community. Soils are typically moist environments with low carbon content that support diverse soil microbial populations. The rhizo-microbiome's microbes are involved in nutrient acquisition and assimilation, improved soil texture, and extracellular substances such as hormones, secondary metabolites, antibiotics, and different signal chemicals are secreted and modulated, all of which leads to improved plant development. The microbes and compounds they produce are bio stimulants that help plants respond to stress. Studies have demonstrated that inoculating plants with plant-growth-promoting rhizobacteria (PGPR) or treating plants with microbe-to-plant signal molecules is an effective way to stimulate crop development. The goal of this review is to highlight the various ways in which plant growth promoting microorganisms (PGPM) can be used to improve crop production under drought stressed condition. The most up-to-date information on microbial inoculant technology is discussed. As a result, a deeper understanding of the mechanisms that determine the composition and structure of microbial communities, as well as the involvement of the host in the recruitment and management of its microbiome, is critical. Plant defence mechanisms, in particular, appear to provide a layer of protection against pathogens while also actively managing the makeup of the general microbiome, according to a growing body of studies. Plants detect water deficits at their roots and send a signal to their shoots, which cause them to synthesize abscisic acid (ABA) in their leaves. ABA is a crucial phytohormone that controls physiological and molecular responses to drought stress, including stomatal closure, gene expression, and osmo-protectants and stress proteins accumulation. The initial stage in the propagation of synthesized ABA is through ABA transporters. ABA inflow in guard cells is sensed by numerous protein kinases that regulate stomatal closure, such as SnRK2s and MAPKs, to limit water loss. To develop drought stress resistance in entire tissues, ABA mediates a wide array of gene expression machines using stress-responsive transcription factors like DREBs and AREBs. We present an overview of current research into the mechanisms used by the plant host to select and control its microbiome in this review. Recent research on the role of keystone microbial species, phytohormones, and abiotic stress in plant-driven dynamic microbial structure is reviewed in detail.

Key words: Drought stress alleviation, Beneficial Microbes- PGPR, PGPF, AMF, Crop improvement

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Many stress factors (both biotic and abiotic) affect a plant's development and productivity during its life cycle, including pathogenicity, competitiveness, drought, salinity, lack of or excessive quantities of essential elements, heavy metals, and high/low temperature. Drought is a major abiotic stress that mostly affects dry and semiarid lands, which

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account for around one-third (49 million km^2) of the world's land surface [1-2]. Drought is one of the primary causes of food production reductions around the world [3-4]. Different definitions of drought have been proposed because to differences in hydro-meteorological variables, socio-economic considerations, and the stochastic character of water needs in different parts of the world [5-6]. Drought definitions are grouped into four kinds according on the variable used to define it: (1) A meteorological drought is defined as a period of time when there is no precipitation. (2) A shortage of sufficient surface and subsurface water resources for established water usage is referred to as a hydrological drought (3) socio-economic drought, defined as a period in which water assets frameworks fail to meet water demands, and (4) agricultural drought, defined as a period in which soil moisture declines, resulting in crop failure [5]. The focus of this review is on agricultural drought. Drought is one of the biggest constraints to food production around the world, with national cereal production estimated to have decreased by 9–10 percent [5]. Drought is anticipated to wreak havoc on agricultural growth on more than half of the world's arable land by 2050 [7-8]. Drought severity, frequency, and length in cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L.), and corn (*Zea mays* L.) are expected to rise as a result of ongoing global climate change in many crop-producing areas across the world [9-10]. Evaluated the results of published studies covering the years 1980–2015 and found that drought stress reduced maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) yields by roughly 40% and 21%, respectively, on a global scale [11].

The green revolution greatly improved plant production; nevertheless, ever-increasing global population and climate change (which is producing drought stress) are putting a strain on our ability to feed the globe. As a result of the catastrophic losses in crop production caused by drought stress during the previous few decades, there is a worldwide interest in enhancing yield and plant drought resistance. The current study's goal was to combine multiple drought tolerance mechanisms and optimize these processes. Drought stress causes plants to go through morphological, physiological, biochemical, and molecular changes [12]. Plant growth, survival, and productivity are influenced by abiotic and biotic stressors. Drought and excessive salinity are two of the most critical environmental conditions that have a detrimental impact on seed germination, seedling growth and the development, and, as a result, agricultural yield, food quality, and global food security. Stress tolerant plant growth promoting fungus (PGPF) may promote agricultural seed germination, seedling establishment, plant growth, and production under adverse environmental conditions [13-20].

Plant-associated microbial communities, such as mycorrhizal fungi, nitrogen-fixing bacteria, and plant growth-promoting rhizobacteria (PGPR), increase crop productivity and resilience to stress. PGPR bacteria are a diverse group of root-colonizing bacteria with strong root colonization abilities and the ability to create a variety of enzymes and metabolites that assist plants cope with biotic and abiotic stressors. Their contributions to the management of abiotic conditions like drought are only now beginning to be recognized [21]. Rhizobia and arbuscular mycorrhizal (AM) fungi may help the legume *Glycyrrhiza* (licorice) cope with abiotic stress, however the potential benefits these symbiotic microbes provide to their host plant are heavily influenced by environmental conditions. The effects of

single and combined inoculation with a rhizobium *Mesorhizobium tianshanense* Chen and an AM fungus *Rhizophagus irregularis* were investigated in a greenhouse pot experiment. Walker and Schuessler studied the performance of *Glycyrrhiza uralensis* Fisch. seedlings under various water regimes. Drought stress reduced rhizobium nodulation while increasing mycorrhizal colonisation. Additionally, co-inoculation of rhizobium and the AM fungus enhanced nodulation in both well-watered and drought-stressed environments. *Glycyrrhiza* seedling growth was highly dependent on mycorrhizal fungi. Under well-watered conditions, the seedlings showed a negative growth dependency on rhizobium, but under drought stress, they demonstrated a positive response [22]. There is a special need to identify methods that boost plants' drought resistance and allow the growth of crops that meet food demands despite restricted water resources [23-24].

Plant responses and genetic regulation under drought

Drought stress is becoming increasingly important among the several abiotic variables threatening agricultural productivity around the world. Drought is a meteorological phrase that is typically defined as a combination of lower rainfall, dwindling groundwater levels, and limited water supply paired with an increase in temperature [25-26]. Drought tolerance is the result of a number of molecular, cellular, and physiological mechanisms, including the induction/repression of numerous genes that induce osmolyte build up, a better antioxidant system, reduced transpiration, inhibited shoot growth, and reduced tillering [27]. Drought is a significant environmental stressor that has negative consequences for plant growth. To cope with drought, plants have evolved a variety of developmental, morphological, physiological, cellular, and molecular processes [28] (Ye *et al.* 2017). Plant responses to drought resistance are regulated by C$_2$H$_2$ zinc finger proteins in both ABA-dependent and ABA-independent ways. Furthermore, through controlling the amounts of ROS-scavenging activities, proline, H$_2$O$_2$, and other cellular components, C$_2$H$_2$ proteins can improve rice plant drought tolerance.

Rice responds to drought stress by producing ZFP245, a C$_2$H$_2$-type zinc finger protein. Rice roots, stems, leaves, and panicles all express ZFP245 [29]. The ZFP245 protein, which has a DLN-box/EAR-motif at its C-terminus, is a trans-activator that is found in the nucleus. It was discovered that overexpression of ZFP245 improved rice's drought tolerance. In plants, ABA plays a crucial role in the osmotic stress response. Exogenous ABA sensitivity was increased in ZFP245-overexpressing rice, implying that ZFP245 plays a role in stress responses via an ABA-dependent pathway. ZFP245 also enhanced the expression of OsP5CS, which encodes a P5CS, and OsProT, which encodes a proline transporter, when stressed. Under drought stress, ZFP245 was also expressed in rice seedlings. Overexpression of ZFP245 enhanced the levels of superoxide dismutase (SOD) and peroxidase (POD), suggesting that ZFP245 may improve rice drought tolerance by activating the ROS scavenging system. ZFP245 also raised the amount of proline in rice plants, possibly resulting in higher resistance to oxidative stress [30]. In *Arabidopsis*, the C$_2$H$_2$ zinc finger protein ZAT18 is transcriptionally activated by dehydration stress. Under drought stress, ZAT18-overexpressing plants lost less water and had more water in their leaves than control plants. Plants overexpressing ZAT18 were also more resistant to stress,

with lower levels of electrolyte leakage and malonic dialdehyde (MDA). After drought stress, ZAT18-overexpressing plants had significantly lower levels of H_2O_2 and much higher levels of POD and SOD activity. These findings suggested that ZAT18 plays a favourable effect in drought tolerance in Arabidopsis [31-32] identified a new type of C_2H_2 zinc finger protein gene from sweet potato called IbZFP1 that is drought-responsive. IbZFP1 works as a transcriptional activator and is found in the nucleus. NaCl, PEG, and ABA treatments all induced IbZFP1 [33]. In transgenic Arabidopsis plants, overexpression of IbZFP1 greatly improved salt and drought tolerance. IbZFP1 overexpression increased the expression of genes involved in ABA signalling, proline biosynthesis, and ROS scavenging in response to salt and drought stress. The transgenic overexpression lines showed enhanced activity of 9-cis-epoxy-carotenoid dioxygenase, pyrroline-5-carboxylate synthase, superoxide dismutase, catalase, ascorbate peroxidase, and peroxidase. ABA, proline, soluble sugars, and chlorophyll levels were all significantly higher, but H_2O_2 and MDA levels were much lower. Under salt and drought stress, the levels of both LEA gene transcripts and LEA proteins rose in IbZFP1-overexpressing Arabidopsis seedlings [34]. Plants with the IbZFP1 gene may be able to withstand abiotic stressors better. In rice, the drought tolerance (DST) gene encodes a zinc finger transcription factor belonging to the C_2H_2 subclass. DST expression was suppressed in response to drought and salt stress. DST mutations resulted in the down-regulation of peroxidase 24 precursor (a H_2O_2 scavenger), resulting in H_2O_2 build up in guard cells, which enhance stomatal closure, reducing water loss and increasing tolerance to drought stress. DST's effect in response to salt and drought conditions was independent of ABA, and it differed from the ABA-induced H_2O_2 build up route in modulating stomatal closure [35]. Plants are sessile organisms that must adapt to harsh environmental circumstances in order to survive and flourish. Various mobile molecules are necessary to transfer extracellular stimuli from the detecting tissue to the target in higher plants in order to ensure optimal growth maintenance. Local and long-distance transmission via small molecules is critical in land plants for preventing water loss by transpiration from guard cells and adapting to drought stress [36-37]. The detection of water deficit signals, as well as the physiological, cellular, and molecular responses, have all been studied extensively in plants in response to drought stress. Plants detect water deficits at their roots and send a signal to their shoots, causing them to synthesise abscisic acid (ABA) in their leaves. ABA is a crucial phytohormone that governs physiological and molecular responses to drought stress, including stomatal closure, gene expression, and osmo-protectants and stress proteins accumulation. The initial stage in the propagation of synthesised ABA is through ABA transporters. ABA inflow in guard cells is sensed by numerous protein kinases that regulate stomatal closure, such as SnRK2s and MAPKs, to limit water loss. To develop drought stress resistance in entire tissues, ABA mediates a wide array of gene expression machines with stress-responsive transcription factors, such as DREBs and AREBs. Drought stress signalling, with a focus on gene networks linked to ABA-related cellular and intercellular responses during drought stress. ABA, a phytohormone, is a crucial role in drought stress avoidance, adaptation, and resistance [38] (Fig 1).
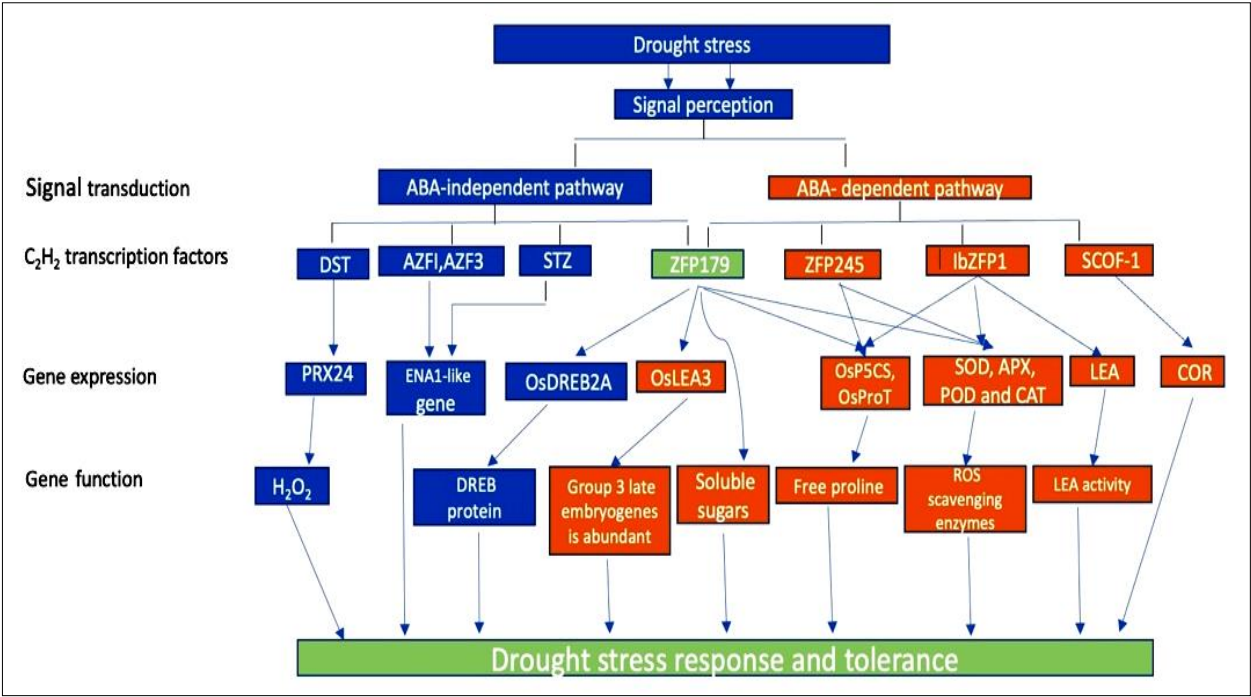

Fig 1 Drought stress response and tolerance (Wang *et al*. [39])

Abbreviations – ABA – Abscisic acid , DST- Drought and Salt tolerance, AZF- Arabidopsis zinc-finger protein; STZ-Salt tolerance zinc finger; SCOF-1- Soybean cold-inducible ; ENA1- Encoding a Na^+-ATPase; COR-Cold-regulated; SOD- Superoxide dismutase; LEA- Late embryogenesis abundant group ; ROS- Reactive oxygen species; POD- Peroxidase ; DREBA2A- Dehydration-responsive element binding 2A ; ZFP179- Zinc finger protein 179 ; CBF-C-repeat-binding factor ; CTR - C-repeat; DRE, dehydration element ; DST- Drought and salt tolerance ; maC_2H_2 - Multiple-adjacent-C_2H_2 ; MDA - Malonic dialdehyde ; P5CS - Delta 1-pyrroline-5-carboxylate synthetase ; ProT - Proline transport; C_2H_2 zinc finger ; spC_2H_2 - Separated-paired-C_2H_2 ; TaZNF - *Triticum aestivum* predicted Dof zinc finger protein ; tC_2H_2 - Triple-C_2H_2.

Microorganisms (pgpr, pgpf, amf): Supporting plant performance under drought stress

The soil is a living, dynamic matrix that is important not just for agriculture and food security, but also for the survival of all life processes. Thousands of bacterial species are found in the soil. Plant growth promoting rhizobacteria (PGPR) are root colonization bacteria (*rhizobacteria*) that promote plant growth through direct or indirect methods. Endophytic and epiphytic bacteria that colonize roots have been shown to affect soil security [40-41]. Drought-stressed seed germination [42], and techniques for clean-up [43]; alienate pathogens; reduce plant diseases; improve plant resistance to diseases, salt stress, cold, and heavy metal toxicity; and improve crop growth, development, yield, and quality by directly synthesizing hormones, antibiotics, and other secondary metabolites, as well as by regulating plant related gene expression and others [44-48].

Interactions between plants and soil microbiomes are in high demand all around the world. Plant growth-promoting rhizobacteria (PGPR) are bacteria that invade plant roots or the rhizosphere and boost plant development directly through nutrient immobilization or by acting as a defence regulator. Over the last few decades, PGPR has established itself as a viable eco-friendly alternative to chemical fertilizers. As a result, they're widely used in agriculture, horticulture, forestry, and environmental cleaning efforts. In natural and agricultural soils, a variety of abiotic and biotic variables influence rhizosphere ecology, and these factors can vary the effects of PGPR on plant health. Manipulation of the rhizospheric microbiome by rhizo-engineering has emerged as a modern tool for understanding the structural, functional, and ecological behaviour of PGPR populations in the rhizosphere [49].

Also, drought stress has become a severe limiting factor for plant productivity and seedling growth, in addition to climate change. The symbiosis of arbuscular mycorrhizal fungi (AMF) has been proposed to promote plant growth and water efficiency in low-water conditions. Under well-watered and water-deficient situations, Caucasian Hackberry (*Celtis Caucasica* L.) seedlings inoculate with mycorrhizal fungus *Rhizophagus intrara*dices and *Funneliformis mosseae*. For 90 days, mycorrhizal and non-mycorrhizal seedlings were treated with 75 percent FC (control), 50, and 25 percent FC. Under regular irrigation and drought treatments, the plant growth parameters dry shoot weight, leaf area, seedling height, dry root weight, length of root, number of secondary roots, and chlorophyll content were higher in mycorrhizal seedlings than in non-inoculated seedlings. H_2O_2 and malondialdehyde (MDA) levels in leaves were reduced by the AMF symbiosis. Surprisingly, there was a positive association between colonization rate and plant growth as well as antioxidant enzyme activity [50]. Plant growth, survival, and productivity are influenced by abiotic and biotic stressors.

Chemical fertilizers and other agrochemicals have been used indiscriminately in the drive to improve agricultural yields due to increased pressure on food production. Synthetic agrochemicals have been shown to have negative environmental effects, and biofertilizers are developing as a viable alternative. Biofertilizers are environmentally friendly fertilizers that help crops grow and yield. They are made up of active or dormant microorganisms that are applied to soil or used to treat agricultural seeds. Rhizobacteria is one of the leading contenders in this regard [51] (Fig 2).
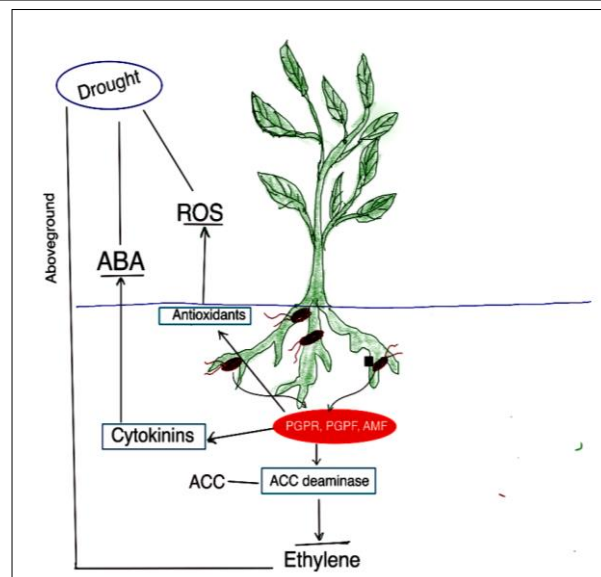

Fig 2 PGPR, PGPF, AMF-induced systemic tolerance to drought stress. Under stress, PGPR, PGPF, AMF secretes cytokinin antioxidants, and ACC deaminase destroys ACC and inhibits ET synthesis. (Lephatsi *et al*. [52])

Drought-stressed performance by PGPR

A plant bio stimulant is any substance or microorganism that is supplied to plants with the purpose of enhancing nutrient efficiency, abiotic stress tolerance, and/or crop quality features, regardless of its nutrient content [53]. Within the taxonomic, functional, and ecological variety of agricultural bio stimulants, there are two basic types to consider: (i) *Rhizobium* endosymbionts that are mutualistic and (ii) Rhizospheric PGPR ('plant growth-promoting rhizobacteria') that are mutualistic. *Rhizobium* and related taxa are sold as biofertilizers, which are microbial inoculants that make it easier for plants to get nutrients. The biology and agricultural applications of Rhizobium-based symbioses have been thoroughly studied in scientific journals and textbooks. PGPRs are multifunctional proteins that affect all aspects of plant life, including nutrition and growth, morphogenesis and development, biotic and abiotic stress responses, and interactions with other organisms in agroecosystems [54-61]. Several of these tasks are performed by the same species, while others are strain-specific or reliant on synergistic interactions within bacterial consortia. The intricacy of PGPRs, as well as the varying responses of plant cultivars and receiving settings, limit their usage in agriculture. In addition, the technical problems connected with inoculant formulation leads to variable results in practice [62-63]. Despite this, the global market for bacterial bio stimulants is expanding, and PGPR inoculants are now thought of as plant 'probiotics,' or effective contributors to plant nutrition and immunity [64].

By direct or indirect methods, PGPR-based biostimulants improve nutrient uptake and drought resistance, as well as crop quality [65]. *Pseudomonas, Bacillus, Enterobacter, Klebsiella, Azobacter, Variovorax, Azosprillum,* and *Serratia* are among the several registered PGPR formulations on the market [66-71], but the use of PGPR in agriculture is only a small part of global agricultural practice [72].

Plant roots emit a wide range of organic nutrients (organic acids, phytosiderophores, sugars, vitamins, amino acids, nucleosides, mucilage) and signals that attract microbial communities, particularly those that can

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metabolize plant-exuded chemicals and thrive in this microbial habitat [73-74]. The rhizospheric soil bacteria that surround the plant root compete for this nutritional benefit, affecting the plant's development, yield, and defence systems as free-living microbes or in a mutualistic interaction with the plant root (endophytic/epiphytic) [75]. Plant development is influenced by these rhizobacteria. When reintroduced by plant inoculation in a soil with competing microflora, about 2–5% of rhizobacteria have a good influence on plant development and are referred to be plant growth promoting rhizobacteria (PGPR). The direct mechanism, which encourages plant development directly in a direct mode, is the most common method of action for PGPR. Nitrogen fixation, phytohormone synthesis, phosphate solubilization, and increased iron availability are all part of this plant growth promotion mechanism. By removing pathogens or triggering plant defensive responses, PGPR can indirectly improve plant development [76-83].

Drought-stressed performance by AMF

Several components of plant physiology are negatively affected by environmental conditions such as water shortages, salinity, and plant diseases. For example, it causes photosynthesis to be uncoupled, enzyme structure to be disrupted, and nutrient uptake and/or transport to the shoot to be reduced, resulting in a hormonal and nutritional imbalance in the plant. Furthermore, drought stress causes osmotic stress, which can lead to turgor loss, which inhibits plant growth and development. Drought stress also causes the creation of reactive oxygen species (ROS), which causes oxidative damage to carbohydrates, protein synthesis, and lipid metabolisms in plants, as well as membrane damage and cell death [84]. Drought stress is a significant abiotic element that limits plant growth and ecosystem production all around the planet [85]. Plant growth is slowed as a result of a shortage of moisture at the whole-plant level, which causes reductions in leaf size, stem extension, and root propagation, as well as disrupting plant water relations and lowering water efficiency. CO_2 absorption by leaves decreases at the cellular level due to stomatal closure, membrane damage, and altered enzyme activity [86]. The production of reactive oxygen species (ROS) causes lipid peroxidation, which increases membrane permeability [87-89]. The first result of drought stress is the build-up of reactive oxygen species (ROS) [90]. ROS generation at excessive amounts can harm the photosynthetic system and other vital activities of cells by damaging oxidative lipids, proteins, and nucleic acids, causing oxidative damage [91]. The end product of peroxidation of unsaturated lipids in the cell is malondialdehyde (MDA). As a result, it's a good biomarker for determining how much lipid peroxidation is generated by oxidative stress in the cell [92-94]. Plants demonstrate a wide range of responses to drought resistance at the whole plant, cellular, and molecular levels as a complicated phenomenon [95-97]. A common mechanism for detoxifying generated ROS during stress response is the ROS-scavenging enzymatic system, which includes catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) [98-100]. Plant–organism symbioses are an important ecological component for bettering plant development in mistreated habitats [101]. Arbuscular mycorrhizal fungi (AMF) have recently been studied for their critical functions in the vine, citrus, apple, peach, strawberry, and other plants [102-104]. Furthermore, some researches have demonstrated that the activation of

antioxidant enzymes in host plants by AMF symbiosis may be attributable to mycorrhization's growth-stimulating effects under drought stress [105-107]. The AMF are obligatory symbionts and ubiquitous soil microorganisms that provide a direct relationship between soil and roots [108-109]. Plant mineral nutrition, water acquisition, and tolerance to biotic and abiotic stressors are all improved by AMF [110-111]. However, the mycorrhizal association is a reforestation approach that has become increasingly popular in recent years [112-113]. Mycorrhizal fungi have been shown to improve plant tolerance to abiotic stress like drought and salinity, as well as biotic stress like infections [114-115]. The amount of water in the soil has a significant impact on spore germination; as a result, mycorrhizal formation and development should be adjusted accordingly [116]. Despite the fact that limiting soil water resources had a negative influence on the number of AMF hyphae, the AMF nevertheless increased host plant nutrient intake [117-118]. Drought stress affects root colonisation in different ways depending on the severity and frequency of the drought [119]. In an experiment, *Citrus sinensis* Osbeck grafted on *Poncirus trifoliata* was exposed to a short-term (up to six days) soil water shortage, which resulted in a non-significant reduction of root mycorrhizal colonisation by *Glomus versiforme* [120]. The importance of mycorrhiza in drought stress reduction has long been recognised, and among the most well-known benefits for host plants are enhanced nutritional status and reduced water deficit damage [121-124. The goal of this study was to see how the AMF-symbiosis affected the morphology and enzymatic antioxidant scavenging system of *Celtis caucasica* seedlings when they were water-stressed [125].

Drought stress alleviation by PGPF

Crop plants are subjected to a variety of abiotic stressors, such as high temperatures, drought, salt, flooding, and heavy metal deposition, all of which have a direct impact on crop plant growth and productivity [126-127]. Most cultivated lands are subjected to one or more of the aforementioned stresses, which can reduce crop plant yields by up to 70% [128]. Climate change threatens the future production of crop plants, particularly cereal crop plants, posing a serious threat to food security [129]. Root construction modifications, mineral solubilization from dead organic substances, and (secondary) metabolite production have all been linked to PGPF-mediated growth promotion in plants under stress or pressure [130]. The naturally occurring PGPF in the soil system has the ability to enhance the plant's immune system and improve plant growth under stressful situations [131]. *Trichoderma sp.* evoked abiotic stress resistance in response to phytopathogen-induced biotic pressure [132]. *T. atroviride* treatment boosted maize plant drought tolerance by increasing antioxidant enzyme machinery [133]. Treatment with *T. hamatum* induced growth and drought tolerance in *Theobroma cacao*. With increased antioxidant enzyme defence machinery, *T. harzianum* treatment reduced salt (NaCl) tolerance capacity in Indian mustard plants [134]. With an increase in relative water content and a decrease in transpiration rate, *T. harzianum* treatment boosted the drought tolerance ability of *N. tabacum* plants [135]. Antibiotic production, mycoparasitism, opposition, and ISR activation are also elicited [136]. Plants' cell walls are strengthened by PGPF, which inhibits solute leakage during abiotic stress [137]. Callose formation during stress promotes sieve pore

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clogging and improves plasma membrane deposition and cell wall apposition [138]. Lignin has a role in plant defence against a variety of pathogens, including pests, and its action is amplified in plants when stress tolerance is induced (heavy metals, salt, high or low temperature, drought, and other stresses [139]. PGPF achieves saline tolerance by increasing sterol content for fatty acid enzyme modification [140-141].

Molecular mechanism of microorganism aided drought tolerance

Crop productivity, food quality, and global food security are all severely hampered by biotic and abiotic stressors. Stress affects a variety of plant factors, including physiological, biochemical, and molecular. Because inorganic fertilizers and pesticides are used in agriculture, soil fertility is depleted and pollution occurs. As a result, safer and more long-term agricultural production methods must be developed. Under such circumstances, the use of plant growth promoting microorganisms (PGPM) and mycorrhizal fungi can help plants thrive. It provides a cost-effective and environmentally friendly solution for safeguarding plants from stress Plant growth may be aided by PGPM, which regulates plant hormones and improves nutrition [142]. The use of stress-tolerant PGPM and AM fungi may improve plant growth and survival under harsh conditions [143]. Microbes exploited indirect and direct ways to support plant growth and development amid stressful situations. Microbes use a variety of biochemical and molecular pathways to promote growth and development [144]. PGPM produces compounds that lower pathogen populations in the plant's environment. Siderophore produced by these bacteria in the rhizosphere, for example, lowered iron availability to certain diseases, limiting their growth [145]. They also help plants grow by fixing nitrogen from the air, solubilizing phosphate, and generating plant hormones [146]. Nutrient mobilization, exopolysaccharide formation, and rhizobitoxine production are some of the other methods [147] that assist the plant in coping with its unfavourable surroundings Rhizobitoxine inhibits the production of ethylene, which helps plants grow and develop in stressful situations [148]. In addition, important enzymes such as ACC-deaminase, chitinase, and glucanase may have the ability to improve plant growth and development under stress conditions [149]. Furthermore, some bacteria have sigma factors that allow them to modify gene expression in unfavourable conditions to counteract harmful effects [150]. Aside from PGPM, another crucial aspect of growth and development is the interaction of fungi with the root of the higher plant. AM is the most frequent type of *mycorrhizae* found in agricultural fields. These fungi are crucial players in nutrient cycle, absorption, and translocation. These microbial processes assist the plant in maintaining its current growth in a stressful environment by reducing the detrimental effects of stress on plant growth and development. As a result, the PGPM were discovered to be a viable alternative to inorganic fertilizers and insecticides. As a result, the plant-microbe interaction may be significant for future food security and sustainable agriculture [150].

Drought is widely acknowledged as a major environmental stress that has piqued the interest of environmentalists and agricultural scientists alike. It is a major agricultural issue that limits plant growth and output all around the world. Drought stress affects almost all of the world's major agricultural lands. It has a wide range of consequences on human society, including the economy [151-152]. Various growth factors as well as stress response genes are affected by drought stress. Limited water content affects cell size and membrane integrity, produces reactive oxygen species, and promotes leaf senescence, all of which contribute to lower agricultural output [153]. Despite this, plants endure a variety of physiological and molecular changes when they are deprived of water, including an increase in ethylene production, a change in chlorophyll concentration, damage to the photosynthetic system, and inhibition of photosynthesis [154]. Drought stress also causes an accumulation of free radicals, which can lead to changes in membrane function, protein folding, lipid peroxidation, and ultimately cell death [155]. Droughts are expected to become more frequent and intense as a result of climate change. Drought stress tolerant microorganisms have the potential to improve plant growth and development when there is a lack of water. Microbes have evolved, adapted, and/or acquired a tolerance mechanism that allows them to thrive in low-water-potential situations. They can build thick walls or go inactive, gathering osmolytes and creating exopolysaccharides (EPS) in the process. These plant-associated microorganisms have a variety of ways for dealing with the negative effects of drought on both plants and soil. They give fertilizer and superior environmental conditions for ongoing plant growth, regardless of water content. Beneficial microorganisms that colonize the rhizosphere enhance plant growth and development in a variety of ways, both directly and indirectly. Among the possible mechanisms are: (1) Phytohormones such as indole-3-acetic acid (IAA), cytokinins, and abscisic acid (ABA) are produced; (2) Bacterial exopolysaccharides are produced. (3) Systemic tolerance was induced by ACC deaminase (4) Phytohormones produced by plants play a significant role in growth and development [156]. In stressful situations, PGPR can also produce plant hormones that encourage plant growth and division. During drought stress, IAA, auxin that regulates vascular tissue differentiation, adventitious and lateral root differentiation, cell division, and shoot growth [157]. ABA is a key growth regulator in drought-stressed plants. When PGPR is introduced into a seed or plant, the concentration of ABA rises, regulating plant physiology to withstand drought stress. Drought stress is alleviated by ABA through modulating root hydraulic conductivity and the transcription of drought-related genes [158]. For example, *Azospirillum brasilense*, improves *Arabidopsis thaliana's* drought tolerance mostly through increased ABA levels [159]. During times of stress, the 1-aminocyclopropane-1-carboxylate (ACC) is a direct precursor of ethylene. ACC is hydrolyzed by bacterial ACC deaminase into ammonia and alphaketobutyrate [160]. Drought stress tolerance and PGPR improve biomass, water potential, and decrease water loss in stressed maize plants. These inoculants reduce antioxidant activity while increasing proline, free amino acid, and sugar synthesis in plants [161]. The chlorophyll concentration in soybean plants falls when there is a lack of water, reducing photosynthesis. To combat this, inoculation of Pseudomonas putida H- 2-3 is required, which alleviates drought stress by increasing chlorophyll content, increasing shoot length, and increasing biomass [162]. Furthermore, combining endophytic and rhizospheric PGPR improves stress tolerance abilities. Microbe-produced exopolysaccharide improves drought tolerance in some plants. For example,

when three drought-tolerant bacterial strains, Maize plants were inoculated with *Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and *Alcaligenes faecalis* (AF3), through the proline content, they demonstrated a potential rise in relative water content, protein, and sugar [163]. In order to survive in such drought conditions, bacteria develop a number of physiological, biochemical, and molecular mechanisms to protect themselves. They produce EPS, a compatible solute, and spore development [164-165] found that bacteria that produce EPS render plants resistant to water during drought stress. During drought stress, compatible solutes such as glycine, proline, betain, and trehalose accumulate, assisting bacteria in maintaining membrane permeability, enzyme integrity, and protein function. Plant growth, nitrogen uptake, and relative water content are all enhanced by mycorrhizal inoculation combinations with particular bacteria, reducing the impact of drought. Because of the increase of proline in the shoot and root, the combination of *Pseudomonas putida* and *Bacillus thuringiensis* reduces stromal conductivity and electrolyte leakage [166]. On the basis of the foregoing explanation, it is obvious that plants with drought-tolerant microbial communities can maintain adequate development and survival in drought conditions.

Regulation of the drought-responsive genes

Drought avoidance and/or drought tolerance mechanisms, which include morphological, physiological, and molecular responses, are used by plants to cope with drought deficient conditions [167-168]. Identifying essential regulators capable of enhancing plant drought tolerance has taken a lot of time and effort, and - to date AREB/ABF [abscisic acid (ABA)-responsive element binding proteins/factors], DREB/CBF (drought-responsive cis-element binding protein/C-repeat-binding factor), and NAC [no apical meristem] (NAM) were discovered to play critical functions. In influencing the expression of an array of drought-responsive genes (DRGs), Arabidopsis activation factor (ATAF) and cup-shaped cotyledon (CUC)] [168]. However, ectopic expressions of these regulators found to be insufficient for creating drought tolerant (or resistant) plants, as they hampered plant development and yield potential. Drought tolerance was mediated primarily by increasing stomata closure (to reduce water evaporation), which inhibited photosynthesis and resulted in growth retardation in transgenic plants constitutively over-expressing the drought-regulated TFs and their target DRGs [169]. As a result, recent research has begun to look into fine-tuning DRG expression in certain temporal and spatial patterns in order to avoid deleterious consequences on the host. These efforts are beginning to provide positive results in improved yields in a number of crops under various water-deprivation conditions in experimental setups [170]. However, none of the research have yet to discover commercial-grade transgenes (DRGs) that improve crop production in both drought and ideal conditions. As a result, there is a pressing need to look into additional options for ensuring long-term crop production in the face of drought [171]. A lack of water has a deleterious impact on various elements of plant physiology [172]. For example, it causes photosynthesis to be uncoupled, enzyme structure to be disrupted, and nutrient uptake and/or transport to the shoot to be reduced, resulting in a hormonal and nutritional imbalance in the plant [173-175]. Furthermore, drought stress causes osmotic stress, which can lead to turgor loss,

which inhibits plant growth and development [176]. Drought stress also causes the creation of reactive oxygen species (ROS), which causes oxidative damage to carbohydrates, protein synthesis, and lipid metabolisms in plants, as well as membrane damage and cell death [177-178]. Plants rely heavily on root-associated microorganisms to cope with a variety of environmental stressors, such as drought [179-180]. Arbuscular mycorrhizal fungi (AMF), which are members of the phylum *Glomeromycota*, form a symbiotic connection with their hosts. AMF consume photosynthetic products, such as sugars, from the roots of the host plant [181-182]. AMF not only improves stomatal control while also increasing water and nutrient uptake to alleviate the deleterious effects of drought [183]. For example, under drought stress, AMF-inoculated Poncirus trifoliata and Rosmarinus officinalis plants showed increased stomatal conductance [184-186]. AMF regulates numerous pathways to prevent oxidative damage under drought stress, in addition to increasing water use efficiency (WUE) and represents a possible avenue to improve next-generation agriculture [187]. The development of AMF-mediated processes in response to drought stress involves changes in the level of plant hormones including strigolactones, jasmonic acid (JA), and abscisic acid (ABA), as well as an improvement in plant water status via enhancing hydraulic conductivity [188]. AMF improved plant drought tolerance in *Solanum lycopersicum* by modulating the 14-3-3 genes (TFT1-TFT12) in the ABA signalling pathway and improving plant water relations [189].

Transcription factor mediated responses

Arbuscular mycorrhizal fungi (AMF) help host plants grow more vigorously under stress by mediating a series of complex communication events between the plant and the fungus, which result in increased photosynthetic rate and other gas exchange-related traits, as well as increased water uptake [190]. Beneficial rhizosphere bacteria are increasingly being used for this purpose, for example, for biofertilization, disease and pest management, and the relief of environmental stresses [191-192]. Many strains of *Trichoderma* spp. are plant growth-promoting fungus (PGPF), which can colonise roots and act as opportunistic symbionts. *Trichoderma* spp. can stimulate the plant immune system (induced systemic resistance, ISR) and pre-activate (prime) molecular defence mechanisms against a wide range of diseases in addition to direct biocontrol of soil infections [193-197]. Furthermore, the favourable effects of these PGPF on plant growth and abiotic stress relief have been widely described [198-200]. Several proteomic and transcriptome investigations, primarily on the aboveground section of the plant, have described the cascade of molecular events that characterise the commencement of the plant–*Trichoderma* interaction [201-204]. Pattern recognition receptors (PRRs) sense microbe-associated molecular patterns (MAMPs) and activate MAMPs/DAMPs-triggered immunity (MTI/DTI) [205-206]. Only a few genes that code for receptor/recognition protein–*Trichoderma* elicitor pairings have been identified so far. Effector-triggered immunity (ETI) is thought to be activated by *Trichoderma* effectors [207]. *Trichoderma*-stimulated cell death was seen during root colonisation [208], which is consistent with ETI-induced programmed cell death. Salicylic acid (SA)-mediated and jasmonate (JA)/ethylene (Et)-mediated signalling have been identified as early events initiated by host-Trichoderma recognition, while abscisic acid (ABA)

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and indole-3-acetic acid (IAA) have also been hypothesised to play essential roles [209]. Recent research suggests that regulatory mechanisms such epigenetic (DNA methylation, histone modification) and post-transcriptional (alternative splicing, AS) modifications are important pathogenic modulators [210-211] and may also play a role in forming positive relationships [212]. Higher cytosine DNA methylation has been linked to the reduction of *Burkholderia phytofirmans*-induced plant growth stimulation in potatoes [213], suggesting that DNA (de)methylation may play a role in positive interactions. A recent analysis of AS patterns in various plant species, including tomato, found that 39–70% of multi-exon genes produce at least one splice variant [214] and that most genes involved in plant defence undergo AS during plant–pathogen interactions [215-217]. However, AS is still poorly understood in plants, especially in Solanaceous species [218-219]. Several studies have found that fungal symbiosis improves resilience to a number of stressors, including drought, salinity, herbivory, temperature, metals, and

pathogens [220-222]. AMF may form interdependent links with about 90% of plant species, including flowering plants, bryophytes, and ferns [223-224]. Vesicles, arbuscules, and hyphae generate vesicles, arbuscules, and hyphae in roots, as well as spores and hyphae in the rhizosphere. The formation of a hyphal network by the AMF with plant roots improves root access to a vast soil surface area, resulting in improved plant growth [225]. AMF improves plant nutrition by increasing the availability of numerous nutrients as well as their transfer [226]. AMF improves soil quality by affecting its structure and texture, which in turn improves plant health [227-228]. The breakdown of soil organic materials can be accelerated by fungal hyphae [229]. Plant growth is harmed by drought stress, which affects enzyme activity, ion uptake, and nutrient assimilation [230-231]. Drought stress relief by AMF has been demonstrated in a variety of crops, including wheat, barley, maize, soybean, strawberry, and onion [232-235]. Plant drought resistance may be attributable to the extra-radical hyphae of fungi and the huge volume of soil investigated by roots [236-239].
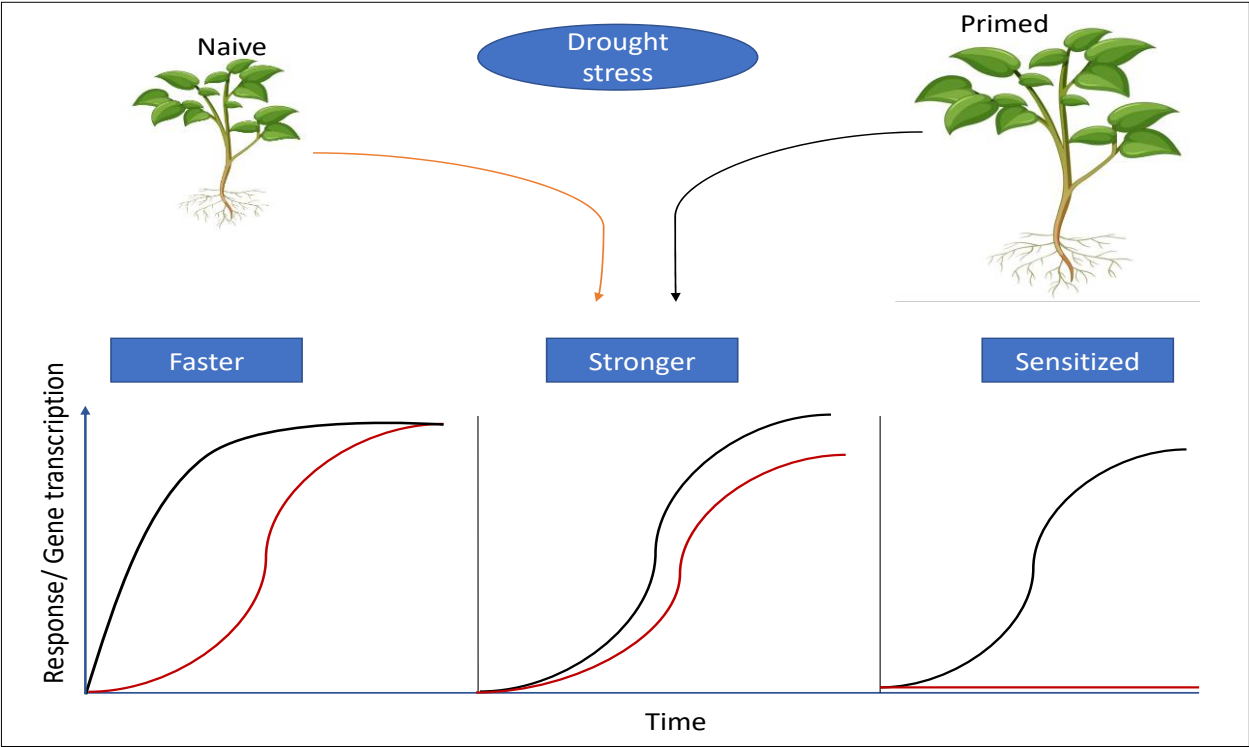

Fig 3 When faced with a stressful situation, priming alters responses. Stress or other priming stimuli, such as microorganisms, can prime a naive plant. Primed and naive plants have different response patterns; a primed plant may respond to stress induction more quickly or robustly than a naive plant. It could also be sensitised, triggering the response at a reduced fitness cost. The primed plant's response mechanisms may be tweaked even more to control a gene network that differs from that of a naive plant (Lephatsi *et al.* [52]

Post-transcriptional modifications and epigenetic control

Plant immunity and defences are preconditioned by PGPR, resulting in increased resistance to abiotic stressors, a phenomenon known as priming. When compared to non-primed plants, the plant responds more quickly and/or robustly to stress in this stage, resulting in better stress tolerance (Fig 3) [240]. The 'primed state,' a state of preparedness achieved, has been related to efficient activation of the defence mechanisms, resulting in increased stress resistance. Various processes, including systemic acquired resistance (SAR) and induced systemic resistance, can be used to describe the increased resistance (ISR). SAR is a defence response mechanism that is activated in the plant's distal sections in response to localized infection

[241], conferring resistance to further stress exposures and priming the plant to fight itself in the event of an attack. ISR, on the other hand, is mediated by microorganisms that mediate plant growth, such as PGPR, which colonize the root system and promote resistance in the plant [242-243]. SAR resistance is induced by the SA response pathway [244], whereas ISR resistance is induced through the ET and JA response pathways. The emergence of SAR and ISR as critical priming mechanisms has been well documented [245-248]. However, there is still a grey region where these priming mechanisms operate. Despite the fact that the processes of priming are unknown, several ideas have been presented, including the accumulation of dormant proteins implicated in signal amplification, such as MAPKs [249].

Following stress perception, transcription factors are activated, enhancing transcription of defense-related genes [250], and epigenetic changes including DNA modifications, histone modifications, or chromatin abnormalities [251]. Plant priming has been proposed as a viable technique for stress regulation since it improves defence responses without compromising a plant's overall fitness, and the resulting stress resistance or tolerance cannot be reversed by microorganisms, resulting in long-term resistance [252]. The chemistry of the rhizosphere and the evolution of plant-rhizomicrobiome interactions are still poorly understood, but new research suggests that certain PGPR species can pre-condition plants for enhanced defence responses to abiotic stressors [253-257].

CONCLUSION

Drought tolerance in primordial terrestrial plants has been retained throughout the evolution of angiosperms, with intense levels restricted to resurrection plants. The fundamental mechanism for maintaining cell turgor is osmotic adjustment, which allows water intake and hence aids in plant metabolic maintenance. In this connection, the association of specific microflora can help the plants conquer the negative effects of plant stress. This review focuses on the ability of these microorganisms to influence the plant responses against drought stress. Therefore, there is a need to undertake more and more studies to understand this complex interaction between the plants and microbiome at the molecular level. Moreover, these beneficial microorganisms are believed to play an important role in the development of biofertilizers for the sustainable improvement of crop production under drought environments. Though several research studies have encompassed the utilization of beneficial microorganisms-PGPR, PGPF, AMF with this objective, but due to several factors the transformation of the same from laboratory to field could not be accomplished satisfactorily.

LITERATURE CITED

1. Prášil I. 1998. Wickens G. E. ecophysiology of economic plants in arid and semi-arid lands. *Biologia plantarum* 41(3).
2. Anjum S, Ashraf U, Tanveer M, Khan I, Hussain S, Shahzad B, Zohaib A, Abbas F, Saleem M, Ali I, Wang L. 2017. Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. *Frontiers in Plant Science* 8: 69.
3. Vinocur B, Altman A. 2005. Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Current Opinion in Biotechnology* 16(2): 123-132.
4. Naveed M, Mitter B, Reichenauer T, Wieczorek K, Sessitsch A. 2014. Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* PsJN and *Enterobacter* sp. FD17. *Environmental and Experimental Botany* 97: 30-39.
5. American Meteorological Society (AMS). 2004. Statement on meteorological drought. *Bulletin of the American Meteorological Society* 85: 771-773.
6. Ngumbi E, Kloepper J. 2016. Bacterial-mediated drought tolerance: Current and future prospects. *Applied Soil Ecology* 105: 109-125.
7. Lesk C, Rowhani P, Ramankutty N. 2016. Influence of extreme weather disasters on global crop production. *Nature* 529(7584): 84-87.
8. Kasim WA, Osman ME, Omar MN, Abd El-Daim IA, Bejai S, Meijer J. 2012. Control of drought stress in wheat using plant-growth-promoting bacteria. *Journal of Plant Growth Regulation* 32(1): 122-130.
9. Europe's Environment—An Assessment of Assessments. 2011. European Environment Agency, Copenhagen.
10. Nature. 2010. How to feed a hungry world. 466(7306): 531-532.
11. Daryanto S, Wang L, Jacinthe PA. 2016. Global synthesis of drought effects on maize and wheat production. *Plos One* 11(5): e0156362.
12. Ilyas M, Nisar M, Khan N, Hazrat A, Khan AH, Hayat K, Fahad S, Khan A, Ullah A. 2020. Drought tolerance strategies in plants: A mechanistic approach. *Journal of Plant Growth Regulation*.
13. de Zelicourt A, Al-Yousif M, Hirt H. 2013. Rhizosphere microbes as essential partners for plant stress tolerance. *Molecular Plant* 6(2): 242-245.
14. Singh DP, Singh HB, Prabha R. 2016. Microbial inoculants in sustainable agricultural productivity. New Delhi: Springer India. 37-60.
15. Hossain MA, Bhattacharjee S, Armin SM, Qian P, Xin W, Li HY, Burritt DJ, Fujita M, Tran LSP. 2015. Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. *Frontiers in Plant Science* 6: 420.
16. Kumar A, Verma JP. 2017. Does plant—Microbe interaction confer stress tolerance in plants: A review? *Microbiological Research* 207: 41-52.
17. Tomer S, Suyal DC, Goel R. 2016. Biofertilizers: A timely approach for sustain- able agriculture. *In*: Choudhary DK, Varma A, Tuteja N. Plant-microbe interaction: An approach to sustainable agriculture. Springer, Singapore. pp 375-395.
18. Vijayabharathi R, Sathya A, Gopalakrishnan S. 2016. A renaissance in plant growth promoting and biocontrol agents by endophytes. *In*: (Eds) Singh DP, Singh HB, Prabha R. Microbial inoculants in sustainable agricultural productivity. Springer, New Delhi. pp 37-60.
19. Vimal SR, Singh JS, Arora NK, Singh S. 2017. Soil-plant-microbe interactions in stressed agriculture management: A review. *Pedosphere* 27(2): 177-192.
20. Yan L, Zhu J, Zhao X, Shi J, Jiang C, Shao D. 2019. Beneficial effects of endophytic fungi colonization on plants. *Applied Microbiology and Biotechnology* 103(8): 3327-3340.

21. Solomon S, Qin D, Manning M, Chen ZS, Marquis FM, Averyt KB, Miller HL. 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, 2007. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge. pp 996.

22. Hao Z, Xie W, Jiang X, Wu Z, Zhang X, Chen B. 2019. Arbuscular mycorrhizal fungus improves rhizobium–glycyrrhiza seedling symbiosis under drought stress. *Agronomy* 9(10): 572.23.

23. Takahashi F, Kuromori T, Sato H, Shinozaki K. 2018. Regulatory gene networks in drought stress responses and resistance in plants. *Advances in Experimental Medicine and Biology*. pp 189-214.

24. Mancosu N, Snyder R, Kyriakakis G, Spano D. 2015. Water scarcity and future challenges for food production. *Water* 7(12): 975-992.

25. Singh D, Laxmi A. 2015. Transcriptional regulation of drought response: a tortuous network of transcriptional factors. *Frontiers in Plant Science* 6: 895.

26. The state of food and agriculture. 2016. Fixers N, solubilizers P. 2016. Fertecon biofertilizers 2016. Rome: FAO. http://www.fao.org/publications/sofa/2016/en/.

27. Pareek A, Sopory SK, Bohnert HJ, Govindjee. 2010. Abiotic stress adaptation in plants. Physiological, Molecular and Genomic Foundation. *Photosynthetica* 48(3): 474-474.

28. Ye Y, Ding Y, Jiang Q, Wang F, Sun J, Zhu C. 2017. The role of receptor-like protein kinases (RLKs) in abiotic stress response in plants. *Plant Cell Reports* 36(2): 235-242.

29. Huang J, Sun SJ, Xu DQ, Yang X, Bao YM, Wang ZF, Tang HJ, Zhang H. 2009. Increased tolerance of rice to cold, drought and oxidative stresses mediated by the overexpression of a gene that encodes the zinc finger protein ZFP245. *Biochemical and Biophysical Research Communications* 389(3): 556-561.

30. Huang J, Wang JF, Wang QH, Zhang HS. 2005. Identification of a rice zinc finger protein whose expression is transiently induced by drought, cold but not by salinity and abscisic acid. *DNA Sequence* 16(2): 130-136.

31. Yin M, Wang Y, Zhang L, Li J, Quan W, Yang L, Wang Q, Chan Z. 2017. The Arabidopsis Cys2/His2 zinc finger transcription factor ZAT18 is a positive regulator of plant tolerance to drought stress. *Journal of Experimental Botany* 68: 2991-3005.

32. Wang F, Tong W, Zhu H, Kong W, Peng R, Liu Q, Yao Q. 2016. A novel Cys2/His2 zinc finger protein gene from sweet potato, IbZFP1, is involved in salt and drought tolerance in transgenic Arabidopsis. *Planta* 243(3): 783-797.

33. Liu Y, Ji X, Nie X, Qu M, Zheng L, Tan Z, Zhao H, Huo L, Liu S, Zhang B, Wang Y. 2015. Arabidopsis Atb HLH 112 regulates the expression of genes involved in abiotic stress tolerance by binding to their E-box and GCG -box motifs. *New Phytologist* 207(3): 692-709.

34. Gao S, Yuan L, Zhai H, Liu C, He S, Liu Q. 2011. Transgenic sweet potato plants expressing an LOS5 gene are tolerant to salt stress. *Plant Cell, Tissue and Organ Culture* 107(2): 205-213.

35. Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX. 2009. A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. *Genes and Development* 23(15): 1805-1817.

36. Steudle E. 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* 52(1): 847-875.

37. Christmann A, Grill E, Huang J. 2013. Hydraulic signals in long-distance signalling. *Current Opinion in Plant Biology* 16(3): 293-300.

38. Abdel-Salam E, Alatar A, El-Sheikh MA. 2017. Inoculation with arbuscular mycorrhizal fungi alleviates harmful effects of drought stress on damask rose. *Saudi Journal of Biological Sciences* 25(8): 1772-1780.

39. Wang K, Ding Y, Cai C, Chen Z, Zhu C. 2018. The role of C_2H_2 zinc finger proteins in plant responses to abiotic stresses. *Physiologia Plantarum* 165(4): 690-700.

40. Ahkami AH, Allen White R, Handakumbura PP, Jansson C. 2017. Rhizosphere engineering: Enhancing sustainable plant ecosystem productivity. *Rhizosphere* 3: 233-243.

41. Wallenstein MD. 2017. Managing and manipulating the rhizosphere microbiome for plant health: A systems approach. *Rhizosphere* 3: 230-232.

42. Delshadi S, Ebrahimi M, Shirmohammadi E. 2017. Influence of plant-growth-promoting bacteria on germination, Growth and nutrients? uptake of *Onobrychis sativa* L. under drought stress. *Journal of Plant Interactions* 12: 200-208.

43. Thijs S, Sillen W, Rineau F, Weyens N, Vangronsveld J. 2016. Towards an enhanced understanding of plant–microbiome interactions to improve phytoremediation: Engineering the meta organism. *Frontiers in Microbiology* 7: 1-15.

44. Gupta G, Panwar J, Jha PN. 2013. Natural occurrence of *Pseudomonas aeruginosa*: a dominant cultivable diazotrophic endophytic bacterium colonizing *Pennisetum glaucum* (L.) R. *Br. Applied Soil Ecology* 64: 252-261.

45. du Jardin P. 2015. Plant biostimulants: Definition, concept, main categories and regulation. *Scientia Horticulturae* (Amsterdam), 196: 3-14.

46. Haymer D. 2015. Genetics and insect pest management in agriculture. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition, and Natural Resources. https://doi.org/10.1079/ PAVSNNR201510049.

47. Kumary KSA, Raj S. 2016. Effect of sett type and intra-row sett spacing on yield of sugar- cane varieties at Metahara Sugar Estate. *International Journal of Advanced Research* 3: 21-26.

48. Vejan P, Abdullah R, Khadiran T. 2016. Role of plant growth promoting rhizobacteria in agricultural sustainability-A review. *Molecules* 21: 1-17.

49. Kumari B, Mallick MA, Solanki MK, Solanki AC, Hora A, Guo W. 2019. Plant growth promoting rhizobacteria (pgpr): Modern prospects for sustainable agriculture. *Plant Health Under Biotic Stress*. 109-127.

50. Sepahvand T, Etemad V, Mohammad M, Shirvany A. 2021. Symbiosis of AMF with growth modulation and antioxidant capacity of Caucasian Hackberry (*Celtis Caucasica* L.) seedlings under drought stress. doi: 10.22034/CAJESTI.2021.01.03.

51. Basu A, Prasad P, Das SN, Kalam S, Sayyed RZ, Reddy MS, El-Enshasy H. 2021. Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: Recent Developments, Constraints, and Prospects.

52. Lephatsi MM, Meyer V, Piater LA, Dubery IA, Tugizimana F. 2021. Plant responses to abiotic stresses and rhizobacterial biostimulants: Metabolomics and epigenetics perspectives. *Metabolites* 11(7): 457.

53. Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, Subramanian S, Smith DL. 2018. Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of bio stimulants for sustainable agriculture. *Frontiers in Plant Science*, [online] 9.

54. Ahmad I, Pichtel J, Hayat S. 2008. Plant-bacteria interactions. Strategies and techniques to promote plant growth. WILEY-VCH Verlag GmbH and Co., KGaA, *Weinheim* 8(5): 553-553.

55. Babalola OO. 2010. Beneficial bacteria of agricultural importance. *Biotechnology Letters* 32: 1559-1570.

56. Berendsen RL, Pieterse CM, Bakker PA. 2012. The rhizosphere microbiome and plant health. *Trends Plant Science* 17: 1360-1385.

57. Berg G, Grube M, Schloter M, Smalla K. 2014. Unraveling the plant microbiome: looking back and future perspectives. *Frontiers in Microbiology* 5: 1-7.

58. Bhattacharyya PN, Jha DK. 2012. Plant growth-promoting rhizobacteria (PGPR): Emergence in Agriculture. *World Journal of Microbiology and Biotechnology* 28: 1327-1350.

59. Gaiero JR, McCall CA, Thompson KA, Dayu NJ, Best AS, Dunfield KE. 2013. Inside the root microbiome: bacterial root endophytes and plant growth. *American Journal of Botany* 100: 1738-1750.

60. Philippot L, Raaijmakers JM, Lemanceau P, Putten WHVD. 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology* 11: 789-799.

61. Vacheron J, Desbrosse G, Bouffaud ML, Touraine B, Moënne-Loccoz Y, Muller D, Legendre L, Wisniewski-Dye P, Rigent-combaret C. 2013. Plant growth-promoting rhizobacteria and root system functioning. *Frontiers in Plant Science* 4: 1-19.

62. Arora NK, Khare E, Maheshwari DK. 2011. Plant growth promoting rhizobacteria: constraints in bioformulation, commercialization, and future strategies. *In*: (Eds) Maheshwari D.K. Plant Growth and Health Promoting Bacteria. Springer, Berlin/Heidelberg. pp 97-116.

63. Brahmaprakash GP, Sahu PK. 2012. Biofertilizers for Sustainability. *Journal of the Indian Institute of Science* 92: 37-62.

64. Jha CK, Saraf M. 2015. Plant growth promoting Rhizobacteria (PGPR): A review. *E3 Journal of Agricultural Research and Development* 5: 108-119.

65. Brown P, Saa S. 2015. Bio stimulants in agriculture. *Frontiers in Plant Science* 6: 671.

66. Nakkeeran S, Fernando WGD, Siddiqui ZA. 2006. Plant growth promoting rhizobacte- ria formulations and its scope in commercialization for the management of pests and diseases. *PGPR Biocontrol Biofertilization*. pp 257-296.

67. Barea JM. 2015. Future challenges and perspectives for applying microbial biotechnology in sustainable agriculture based on a better understanding of plant-microbiome interactions. *Journal of Soil Science and Plant Nutrition* 15(2): 261-282.

68. Bishnoi U. 2015. PGPR interaction: An ecofriendly approach promoting the sustainable agri- culture system. Elsevier Ltd. https://doi.org/10.1016/bs.abr.2015.09.006.

69. Trivedi G, Shah R, Patel P, Saraf M. 2017. Role of endophytes in agricultural crops under drought stress: current and future prospects. ISSN Online: 2349-7785.

70. Van Der Heijden MG, Wiemken A, Sanders IR. 2003. Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytologist* 157(3): 569-578.

71. Le Mire G, Nguyen ML, Fassotte B. 2016. Review: Implementing plant bio stimulants and biocontrol strategies in the agroecological management of cultivated ecosystems review: Implementing plant biostimulants and biocontrol strategies in the agroecological management of cultivated ecosystems. *Biotechnologie, Agronomie, Société et Environnement* 20: 299-313.

72. Meena MK, Gupta S, Datta S. 2016. Antifungal potential of pgpr, their growth promoting activity on seed germination and seedling growth of winter wheat and genetic variabilities among bacterial isolates. *International Journal of Current Microbiology and Applied Sciences* 5(1): 235-243.

73. Ahemad M, Kibret M. 2014. Mechanisms and applications of plant growth promoting rhizo- bacteria: Current perspective. *Journal of King Saud University – Science* 26: 1-20. https://doi. org/10.1016/j.jksus.2013.05.001.

74. Hasan M, Bano A, Hassan SG. 2014. Enhancement of rice growth and pro- duction of growth-promoting phytohormones by inoculation with Rhizobium and other Rhizobacteria. *World Applied Sciences Journal* 31: 1734-1743. https://doi.org/10.5829/idosi. wasj.2014.31.10.364.

75. Yehuda Z, Shenker M, Romheld V, Marschner H, Hadar Y, Chen Y. 1996. The role of ligand exchange in the uptake of iron from microbial siderophores by gramineous plants. *Plant Physiology* 112(3): 1273-1280.

76. Narasimhan K, Basheer C, Bajic VB, Swarup S. 2003. Enhancement of plant-microbe interactions using a rhizosphere metabolomics-driven polychlorinated biphenyls 1 [w]. *Plant Physiology* 132: 146-153. https://doi.org/10.1104/pp.102.016295.populations.

77. Gupta S, Dikshit AK. 2010. Biopesticides: An ecofriendly approach for pest control. *Journal of Biopesticides* 3: 186-188.

78. Gunasekera D, Berkowitz GA. 1992. Heterogenous stomatal closure in response to leaf water deficits is not a universal phenomenon. *Plant Physiology* 98(2): 660-665.

79. He M, He CQ, Ding NZ. 2018. Abiotic stresses: General defenses of land plants and chances for engineering multi stress tolerance. *Frontiers in Plant Science* 9: 1771.

80. Ingram J, Bartels D. 1996. The molecular basis of dehydration tolerance in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 47(1): 377-403.

81. Li XL, George E, Marschner H. 1991. Extension of the phosphorus depletion zone in VA-mycorrhizal white clover in a calcareous soil. *Plant and Soil* 136(1): 41-48.

82. Tariq M, Noman M, Ahmed T. 2017. Antagonistic features displayed by plant growth promoting rhizobacteria (PGPR): A review. *Genetics and Molecular Biology* 35: 38-43.

83. Berninger T, González López Ó, Bejarano A, Preininger C, Sessitsch A. 2017. Maintenance and assessment of cell viability in formulation of non-sporulating bacterial inoculants. *Microbial Biotechnology* 11(2): 277-301.

84. Sohrabi Y, Heidari G, Weisany W, Golezani KG, Mohammadi K. 2012. Changes of antioxidative enzymes, lipid peroxidation and chlorophyll content in chickpea types colonized by different Glomus species under drought stress. *Symbiosis* 56(1): 5-18.

85. Xiao X, Yang F, Zhang S, Korpelainen H, Li C. 2009. Physiological and proteomic responses of two contrasting *Populus cathayana* populations to drought stress. *Physiologia Plantarum* 136(2): 150-168.

86. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development* 29(1): 185-212.

87. Dhindsa RS, Plumb-Dhindsa PAMELA, Thorpe TA. 1981. Leaf senescence: correlated with increased levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide dismutase and catalase. *Journal of Experimental Botany* 32(1): 93-101.

88. Gill SS, Tuteja N. 2010. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry* 48(12): 909-930.

89. Hossain MM, Sultana F, Islam S. 2017. Plant growth-promoting fungi (PGPF): Phytostimulation and Induced Systemic Resistance. Plant-Microbe Interactions in Agro-Ecological Perspectives. pp 135-191.

90. Nath M, Bhatt D, Prasad R, Tuteja N. 2017. Reactive oxygen species (ROS) metabolism and signaling in plant-mycorrhizal association under biotic and abiotic stress conditions. *In*: Mycorrhiza-eco-physiology, secondary metabolites, nanomaterials. pp 223-232.

91. Golldack D, Li C, Mohan H, Probst N. 2014. Tolerance to drought and salt stress in plants: unraveling the signaling networks. *Frontiers in Plant Science* 5: 151.

92. Sofo A, Dichio B, Xiloyannis C, Masia A. 2004. Effects of different irradiance levels on some antioxidant enzymes and on malondialdehyde content during rewatering in olive tree. *Plant Science* 166(2): 293-302.

93. Campo S, Baldrich P, Messeguer J, Lalanne E, Coca M, San Segundo B. 2014. Overexpression of a calcium-dependent protein kinase confers salt and drought tolerance in rice by preventing membrane lipid peroxidation. *Plant Physiology* 165(2): 688-704.

94. Gharibi S, Tabatabaei BES, Saeidi G, Goli SAH. 2016. Effect of drought stress on total phenolic, lipid peroxidation, and antioxidant activity of Achillea species. *Applied Biochemistry and Biotechnology* 178(4): 796-809.

95. Blum A. 2011. Drought resistance–is it really a complex trait? *Functional Plant Biology* 38(10): 753-757.

96. Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought—from genes to the whole plant. *Function Plant Biology* 30(3): 239-264.

97. Fang Y, Xiong L. 2015. General mechanisms of drought response and their application in drought resistance improvement in plants. *Cellular and Molecular Life Sciences* 72(4): 673-689.

98. Mittler R, Vanderauwera S, Gollery M, Van Breusegem F. 2004. Reactive oxygen gene network of plants. *Trends Plant Science* 9(10): 490-498.

99. Bailey-Serres J, Mittler R. 2006. The roles of reactive oxygen species in plant cells. *Plant Physiology* 141(2): 311-311.

100. Cardoso I, Kuyper T. 2006. Mycorrhizas and tropical soil fertility. *Agriculture, Ecosystems and Environment* 116(1/2): 72-84.

101. Requena N, Perez-Solis E, Azcón-Aguilar C, Jeffries P, Barea JM. 2001. management of indigenous plant-microbe symbioses aids restoration of decertified ecosystems. *Applied and Environmental Microbiology* 67(2): 495-498.

102. Ruiz-Lozano JM, Collados C, Barea JM, Azcón R. 2001. Cloning of cDNAs encoding SODs from lettuce plants which show differential regulation by arbuscular mycorrhizal symbiosis and by drought stress. *Journal of Experimental Botany* 52(364): 2241-2242.

103. Krishna H, Das B, Attri BL, Grover M, Ahmed N. 2010. Suppression of *Botryosphaeria* canker of apple by arbuscular mycorrhizal fungi. *Crop Protection* 29(9): 1049-1054.

104. Wu QS, Xia RX, Zou YN. 2006. Reactive oxygen metabolism in mycorrhizal and non-mycorrhizal citrus (*Poncirus trifoliata*) seedlings subjected to water stress. *Journal of Plant Physiology* 163(11): 1101-1110.

105. García-Cristobal J, García-Villaraco A, Ramos B, Gutierrez-Mañero J, Lucas JA. 2015. Priming of pathogenes is related-proteins and enzymes related to oxidative stress by plant growth promoting rhizobacteria on rice plants upon abiotic and biotic stress challenge. *Journal of Plant Physiology* 188: 72-79.

106. Wu QS, Zou YN. 2009. Mycorrhiza has a direct effect on reactive oxygen metabolism of drought-stressed citrus. *Plant Soil Environment* 55(10): 436-442.

107. Latef AAHA, Chaoxing H. 2011. Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress. *Scientia Horticulturae* 127(3): 228-233.

108. Bharti N, Pandey SS, Barnawal D, Patel VK, Kalra A. 2016. Plant growth promoting rhizobacteria *Dietzia natronolimnaea* modulates the expression of stress responsive genes providing protection of wheat from salinity stress. *Scientific Reports* 6(1): 34768.

109. Çakmakçi R, Dönmez MF, Erdoan Ü. 2007. The effect of plant growth promoting rhizobacteria on barley seedling growth, nutrient uptake, some soil properties, and bacterial counts. *Turkish Journal of Agriculture* 31: 189-199.

110. Göhre V, Paszkowski U. 2006. Contribution of the arbuscular mycorrhizal symbiosis to heavy metal phytoremediation. *Planta* 223(6): 1115-1122.

111. Latef AAHA, Hashem A, Rasool S, Abd_Allah EF, Alqarawi AA, Egamberdieva D, Jan S, Anjum NA, Ahmad P. 2016. *Arbuscular mycorrhizal* symbiosis and abiotic stress in plants: A review. *Journal of Plant Biology* 59(5): 407-426.

112. Smith SE, Read DJ. 2008. Mycorrhizal Symbiosis, 3rd Edition; Academic Press: London, UK, 2008.

113. Berruti A, Borriello R, Orgiazzi A, Barbera AC, Lumini E, Bianciotto V. 2014. Arbuscular mycorrhizal fungi and their value for ecosystem management. Biodiversity: the dynamic balance of the planet. *INTECH Open Access Publisher, Rijeka, Croatia.* pp 159-191.

114. Guerrero-Galán C, Calvo-Polanco M, Zimmermann SD. 2019. Ectomycorrhizal symbiosis helps plants to challenge salt stress conditions. *Mycorrhiza* 29(4): 291-301.

115. Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, Satou M. 2002. Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold and high- salinity stresses using a full-length cDNA microarray. *Plant Journal* 31(3): 279-292.

116. Nasim G. 2010. The role of arbuscualr mycorrhizae in inducing resistance to drought and salinity stress in crops. *Plant Adaptation* and *Phytoremediation.* pp 119-141. https://doi.org/10.1007/978-90-481-9370-7_6

117. Van Wees SC, Van der Ent S, Pieterse CM. 2008. Plant immune responses triggered by beneficial microbes. *Current Opinion in Plant Biology* 11(4): 443-448.

118. Cassán F, Maiale S, Masciarelli O, Vidal A, Luna V, Ruiz O. 2009. Cadaverine production by *Azospirillum brasilense* and its possible role in plant growth promotion and osmotic stress mitigation. *European Journal of Soil Biology* 45(1): 12-19.

119. Aroca R, Vernieri P, Ruiz-Lozano JM. 2008. Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. *Journal of Experimental Botany* 59(8): 2029-2041.

120. Wu QS, He XH, Zou YN, Liu CY, Xiao J, Li Y. 2012. Arbuscular mycorrhizas alter root system architecture of *Citrus tangerine* through regulating metabolism of endogenous polyamines. *Plant Growth Regulation* 68(1): 27-35.

121. Subramanian KS, Charest C. 1995. Influence of arbuscular mycorrhizae on the metabolism of maize under drought stress. *Mycorrhiza* 5(4): 273-278.

122. Al-Karaki G, McMichael BZAKJ, Zak J. 2004. Field response of wheat to arbuscular mycorrhizal fungi and drought stress. *Mycorrhiza* 14(4): 263-269.

123. Rapparini F, Peñuelas J. 2014. Mycorrhizal fungi to alleviate drought stress on plant growth. *In Use of Microbes for the Alleviation of Soil Stresses* 1: 21-42.

124. Ruiz-Lozano JM, Porcel R, Azcón C, Aroca R. 2012. Regulation by arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies. *Journal of Experimental Botany* 63(11): 4033-4044.

125. Díaz A, Smith A, Mesa P, Zapata J, Caviedes D, Cotes AM. 2013. Control of fusarium wilt in cape gooseberry by *Trichoderma koningiopsis* and PGPR. (Eds) Pertot I, Elad Y, Barka EA, Clément C. Working Group Biological Control of Fungal and Bacterial Plant Pathogens; IOBC Bulletin: Dijon, France, 86: 89-94.

126. Jin N, Liu SM, Peng H, Huang WK, Kong LA, Wu YH, Chen YP, Ge FY, Jian H, Peng DL. 2019. Isolation and characterization of *Aspergillus niger* NBC001 underlying suppression against *Heterodera glycines*. *Scientific Reports* 9: 591.

127. Choudhary DK, Varma A, Tuteja N. 2016. Plant-microbe interaction: An approach to sustainable agriculture. Singapore: Springer Singapore. pp 375-395.

128. Da K, Nowak J, Flinn B. 2012. Potato cytosine methylation and gene expression changes induced by a beneficial bacterial endophyte, *Burkholderia phytofirmans* strain PsJN. *Plant Physiology and Biochemistry* 50: 24-34.

129. Mantri NL, Ford R, Coram TE, Pang EC. 2007. Transcriptional profiling of chickpea genes differentially regulated in response to high-salinity, cold and drought. *BMC Genomics* 8(1): 303.

130. Shivanna MB, Meera MS, Kubota M, Hyakumachi M. 2005. Promotion of growth and yield in cucumber by *zoysia* grass rhizosphere fungi. *Microbes and Environments* 20(1): 34-40.

131. Murali M, Amruthesh KN, Sudisha J, Niranjana SR, Shetty HS. 2012. Screening for plant growth promoting fungi and their ability for growth promotion and induction of resistance in pearl millet against downy mildew disease. *Journal of Phytology* 4: 30-36.

132. Masunaka A, Hyakumachi M, Takenaka S. 2011. Plant growth-promoting fungus, *Trichoderma koningi* suppresses isoflavonoid phytoalexin vestitol production for colonization on/in the roots of lotus japonicus. *Microbes and Environments* 26(2): 128-134.

133. Saxena A, Raghuwanshi R, Singh HB. 2015. *Trichoderma* species mediated differential tolerance against biotic stress of phytopathogens in *Cicer arietinum* L. *Journal of Basic Microbiology* 55(2): 195-206.

134. Guler NS, Pehlivan N, Karaoglu SA, Guzel S, Bozdeveci A. 201). *Trichoderma atroviride* ID20G inoculation ameliorates drought stress-induced damages by improving antioxidant defence in maize seedlings. *Acta Physiologiae Plantarum* 38(6).

135. Dixit P, Mukherjee PK, Ramachandran V, Eapen S. 2011. Glutathione transferase from *Trichoderma virens* enhances cadmium tolerance without enhancing its accumulation in transgenic *Nicotiana tabacum*. *Plos One* 6(1): p.e16360.

136. Vieira PM, Santos MP, Andrade CM, Souza-Neto OA, Ulhoa CJ, Aragão FJL. 2017. Overexpression of an aquaglyceroporin gene from *Trichoderma harzianum* improves water-use efficiency and drought tolerance in Nicotiana tabacum. *Plant Physiology and Biochemistry* 121: 38-47.

137. Benitez T, Rincon AM, Limon MC, Codon AC. 2004. Bio control mechanisms of *Trichoderma* strains. *International Microbiology* 7: 249-260.

138. Plemenitaš A, Vaupotič T, Lenassi M, Kogej T, Gunde-Cimerman N. 2008. Adaptation of extremely halotolerant black yeast *Hortaea werneckii* to increased osmolarity: a molecular perspective at a glance. *Studies in Mycology* 61: 67-75.

139. Nishimura MT. 2003. Loss of a callose synthase results in salicylic acid-dependent disease resistance. *Science* 301(5635): 969-972.

140. Moura JCMS, Bonine CAV, de Oliveira Fernandes Viana J, Dornelas MC, Mazzafera P. 2010. Abiotic and biotic stresses and changes in the lignin content and composition in plants. *Journal of Integrative Plant Biology* 52(4): 360-376.

141. Turk M, Méjanelle L, Šentjurc M, Grimalt JO, Gunde-Cimerman N, Plemenitaš A. 2004. Salt-induced changes in lipid composition and membrane fluidity of halophilic yeast-like melanized fungi. *Extremophiles* 8(1): 53-61.

142. Fernández-Lizarazo JC, Moreno-Fonseca LP. 2016. Mechanisms for tolerance to water-deficit stress in plants inoculated with arbuscular mycorrhizal fungi. A review. *Agronomía Colombiana* 34(2): 179-189.

143. Fu J, Liu Z, Li Z, Wang Y, Yang K. 2017. Alleviation of the effects of saline-alkaline stress on maize seedlings by regulation of active oxygen metabolism by *Trichoderma asperellum. PLos One* 12: e0179617.

144. Spence C, Bais H. 2015. Role of plant growth regulators as chemical signals in plant–microbe interactions: a double edged sword. *Current Opinion in Plant Biology* 27: 52-58.

145. Złoch M, Thiem D, Gadzała-Kopciuch R, Hrynkiewicz K. 2016. Synthesis of siderophores by plant-associated metallotolerant bacteria under exposure to Cd^{2+}. *Chemosphere* 156: 312-325.

146. Ahmad M, Zahir ZA, Asghar HN, Asghar M. 2011. Inducing salt tolerance in mung bean through coinoculation with rhizobia and plant-growth-promoting rhizobacteria containing 1-aminocyclopropane-1-carboxylat deaminase. *Canadian Journal of Microbiology* 57(7): 578-589.

147. Vardharajula S, Zulfikar Ali S, Grover M, Reddy G, Bandi V. 2011. Drought-tolerant plant growth promoting *Bacillus* spp.: effect on growth, osmolytes, and antioxidant status of maize under drought stress. *Journal of Plant Interactions* 6(1): 1-14.

148. Kumar KV, Srivastava S, Singh N, Behl HM. 2009. Role of metal resistant plant growth promoting bacteria in ameliorating fly ash to the growth of *Brassica juncea. Journal of Hazardous Materials* 170(1): 51-57.

149. Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management. *In*: (Eds) Lichtfouse, E., Navarrete, M., Debaeke, P., V́eronique, S., Alberola, C. Sustainable Agriculture. Springer, Dordrecht Sustainable Agriculture. pp 153-188.

150. Govindasamy V. 2010. *Bacillus* and *Paenibacillus* spp.: Potential PGPR for Sustainable Agriculture. *In*: Maheshwari, D. (Eds.), Plant Growth and Health Promoting Bacteria. Microbiology Monographs 18 Springer, Berlin, Heidelberg.

151. Disante KB, Fuentes D, Cortina J. 2011. Response to drought of Zn-stressed *Quercus suber* L. seedlings. *Environmental and Experimental Botany* 70(2/3): 96-103.

152. Mishra AK, Singh VP. 2010. A review of drought concepts. *Journal of Hydrology* 391(1/2): 202-216.

153. Tiwari S, Lata C, Chauhan PS, Nautiyal CS. 2015. *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. *Plant Physiology and Biochemistry* 99: 108-117.

154. Lata C, Prasad M. 2011. The Role of DREBs in regulation of abiotic stress responses in plants. *Journal of Experimental Botany* 62(14): 4731-4748.

155. Tan G, Liu K, Kang J, Xu K, Zhang Y, Hu L, Zhang J, Li C. 2015. Transcriptome analysis of the compatible interaction of tomato with *Verticillium dahliae* using RNA-sequencing. *Frontiers in Plant Science* 6: 428.

156. Smékalová V, Doskočilová A, Komis G, Šamaj J. 2014. Crosstalk between secondary messengers, hormones and MAPK modules during abiotic stress signalling in plants. *Biotechnology Advances* 32(1): 2-11.

157. Goswami D, Thakker JN, Dhandhukia PC. 2015. Simultaneous detection and quantification of indole-3-acetic acid (IAA) and indole-3-butyric acid (IBA) produced by rhizobacteria from l-tryptophan (Trp) using HPTLC. *Journal of Microbiological Methods* 110: 7-14.

158. Jiang S, Zhang D, Wang L, Pan J, Liu Y, Kong X, Zhou Y, Li D. 2013. A maize calcium-dependent protein kinase gene, ZmCPK4, positively regulated abscisic acid signalling and enhanced drought stress tolerance in transgenic Arabidopsis. *Plant Physiology and Biochemistry* 71: 112-120.

159. Cohen AC, Bottini R, Pontin M, Berli FJ, Moreno D, Boccanlandro H, Travaglia CN, Piccoli PN. 2014. *Azospirillum brasilenseameliorates* the response of *Arabidopsis thalianato* drought mainly via enhancement of ABA levels. *Physiologia Plantarum* 153(1): 79-90.

160. Bal HB, Nayak L, Das S, Adhya TK. 2013. Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. *Plant and Soil* 366(1/2): 93-105.

161. De, E., Promotoras, B. and Bpcv, V. (2015). Efficiency of plant growth promoting rhizobacteria (PGPR). Terra Latinoam, 33, 321–330.

162. Kang SM, Radhakrishnan R, Khan AL, Kim MJ, Park JM, Kim BR, Shin DH, Lee IJ. 2014. Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. *Plant Physiology and Biochemistry* 84: 115-124.

163. Naseem H, Bano A. 2014. Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. *Journal of Plant Interactions* 9(1): 689-701.

164. Chithrashree, Udayashankar AC, Chandra NS, Reddy MS, Srinivas C. 2011. Plant growth-promoting rhizobacteria mediate induced systemic resistance in rice against bacterial leaf blight caused by *Xanthomonas oryzae* pv. oryzae. *Biological Control* 59(2): 114-122.

165. Daly DH, Velivelli SLS, Prestwich BD. 2017. The role of soil microbes in crop biofortification. *In*: Agriculturally Important microbes for sustainable agriculture. (Eds) Meena, V., Mishra, P., Bisht, J., Pattanayak, A. Springer: Singapore.

166. Ortiz N, Armada E, Duque E, Roldán A, Azcón R. 2015. The Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: Effectiveness of autochthonous or allochthonous strains. *Journal of Plant Physiology* 174: 87-96.

167. Parent B, Hachez C, Redondo E, Simonneau T, Chaumont F, Tardieu F. 2009. Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: A Trans-Scale Approach. *Plant Physiology* 149(4): 2000-2012.

168. Candar-Cakir B, Arican E, Zhang B. 2016. Small RNA and degradome deep sequencing reveals drought-and tissue-specific microns and their important roles in drought-sensitive and drought-tolerant tomato genotypes. *Plant Biotechnology Journal* 14(8): 1727-1746.

169. Osakabe Y, Osakabe K, Shinozaki K, Tran LSP. 2014. Response of plants to water stress. *Frontiers in Plant Science* 5: 86. https://doi:10.3389/fpls.2014.00086.

170. Nakashima K, Yamaguchi-Shinozaki K, Shinozaki K. 2014. The transcriptional regulatory network in the drought response and its crosstalk in abiotic stress responses including drought, cold, and heat. *Frontiers in Plant Science* 5: 170.

171. Yang S, Tang F, Zhu H. 2014. Alternative splicing in plant immunity. *International Journal of Molecular Sciences* 15: 10424-10445.

172. Batool A, Akram NA, Cheng ZG, Lv GC, Ashraf M, Afzal M, Xiong JL, Wang JY, Xiong YC. 2019. Physiological and biochemical responses of two spring wheat genotypes to non-hydraulic root-to-shoot signalling of partial and full root-zone drought stress. *Plant Physiology and Biochemistry* 139: 11-20.

173. Selmar D, Kleinwächter M. 2013. Influencing the product quality by deliberately applying drought stress during the cultivation of medicinal plants. *Industrial Crops and Products* 42: 558-566.

174. Ruiz-Lozano JM, Aroca R, Zamarreno AM, Molina S, Andreo-Jimenez B, Porcel R, Garcia-Mina JM, Ruyter-Spira C, Lopez-Raez JA. 2016. Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and improves drought tolerance in lettuce and tomato. *Plant Cell and Environment* 39: 441-452.

175. Xie W, Hao Z, Zhou X, Jiang X, Xu L, Wu S, Zhao A, Zhang X, Chen B. 2018. Arbuscular mycorrhiza facilitates the accumulation of glycyrrhizin and liquiritin in *Glycyrrhiza uralensis* under drought stress. *Mycorrhiza* 28(3): 285-300.

176. Lopes MJ, dos S, Dias-Filho MB, Gurgel ESC. 2021. Successful plant growth-promoting microbes: Inoculation Methods and Abiotic Factors. *Frontiers in Sustainable Food Systems* 5.

177. Atkinson NJ, Urwin PE. 2012. The interaction of plant biotic and abiotic stresses: from genes to the field. *Journal of Experimental Botany* 63(10): 3523-3543.

178. Singh B, Bohra A, Mishra S, Joshi R, Pandey S. 2015. Embracing new-generation "omics" tools to improve drought tolerance in cereal and food-legume crops. *Biologia Plantarum* 59(3): 413-428.

179. Ruiz-Lozano JM, Aroca R. 2010. Modulation of aquaporin genes by the arbuscular mycorrhizal symbiosis in relation to osmotic stress tolerance. *In*: Symbioses and Stress; Springer: Dordrecht, The Netherlands. 17: 357-374.

180. Saia S, Amato G, Frenda AS, Giambalvo D, Ruisi P. 2014. Influence of arbuscular mycorrhizae on biomass production and nitrogen fixation of berseem clover plants subjected to water stress. *Plos One* 9(3): e90738.

181. Mayo S, Gutiérrez S, Malmierca MG, Lorenzana A, Campelo MP, Hermosa R, Casquero PA. 2013. Influence of *Rhizoctonia solani* and *Trichoderma* spp. in growth of bean (*Phaseolus vulgaris* L.) and in the induction of plant defense-related genes. *Frontiers in Plant Science* 16: 69-80.

182. Smith SE, Jakobsen I, Grønlund M, Smith FA. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiology* 156(3): 1050-1057.

183. Auge RM, Toler HD, Saxton AM. 2015. Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: A meta-analysis. *Mycorrhiza* 25: 13-24.

184. Martínez-Medina A, Fernandez I, Lok GB, Pozo MJ, Pieterse CMJ, Van Wees SCM. 2017. Shifting from priming of salicylic acid- to jasmonic acid-regulated defences by *Trichoderma* protects tomato against the root knot nematode Meloidogyne incognita. *New Phytologist* 213(3): 1363-1377.

185. Martínez-Medina A, Fernández I, Sánchez-Guzmán MJ, Jung SC, Pascual JA, Pozo MJ. 2013. Deciphering the hormonal signalling network behind the systemic resistance induced by *Trichoderma harzianum* in tomato. *Frontiers in Plant Science* 4: 1-12.

186. Ruíz-Sánchez M, Armada E, Muñoz Y, García de Salamone IE, Aroca R, Ruíz-Lozano JM, Azcón R. 2011. *Azospirillum* and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. *Journal of Plant Physiology* 168(10): 1031-1037.

187. Chitarra W, Pagliarani C, Maserti B, Lumini E, Siciliano I, Cascone P, Schubert A, Gambino G, Balestrini R, Guerrieri E. 2016. Insights on the impact of arbuscular mycorrhizal symbiosis on tomato tolerance to water stress. *Plant Physiology* 00307.2016.

188. Meena VS, Maurya BR, Verma JP. 2014. Does a rhizospheric microorganism enhance K^+ availability in agricultural soils? *Microbiological Research* 169(5/6): 337-347.

189. Xu L, Li T, Wu Z, Feng H, Yu M, Zhang X, Chen B. 2018. Arbuscular mycorrhiza enhances drought tolerance of tomato plants by regulating the 14-3-3 genes in the ABA signalling pathway. *Applied Soil Ecology* 125: 213-221.

190. Birhane E, Sterck FJ, Fetene M, Bongers F, Kuyper TW. 2012. Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. *Oecologia* 169(4): 895-904.

191. Lopez-Bucio J, Pelagio-Flores R, Herrera-Estrella A. 2015. *Trichoderma* as biosti-mulant: exploiting the multilevel properties of a plant beneficial fungus. *Scientia Horticulturae* 196: 109-123.

192. Rouphael Y, Cardarelli M, Bonini P, Colla G. 2017. Synergistic action of a microbial-based biostimulant and a plant derived-protein hydrolysate enhances lettuce tolerance to alkalinity and salinity. *Frontiers in Plant Science* 8: 131.

193. Shoresh M, Harman GE. 2008. The molecular basis of shoot responses of maize seedlings to *Trichoderma harzianum* T22 inoculation of the root: a proteomic approach. *Plant Physiology* 147: 2147-2163.

194. Tucci M, Ruocco M, De Masi L, De Palma M, Lorito M. 2011. The beneficial effect of *Trichoderma* spp. on tomato is modulated by the plant genotype. *Molecular Plant Pathology* 12: 341-354.

195. Hermosa R, Viterbo A, Chet I, Monte E. 2012. Plant-beneficial effects of *Trichoderma* and of its genes. *Microbiology* 158: 17-25.

196. Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Van Wees SCM, Bakker PAHM. 2014. Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology* 52(1): 347-375.

197. Naamala J, Smith DL. 2020. Relevance of plant growth promoting microorganisms and their derived compounds, in the face of climate change. *Agronomy* 10(8): 1179.

198. Brotman Y, Landau U, Cuadros-Inostroza Á, Takayuki T, Fernie AR, Chet I, Viterbo A, Willmitzer L. 2013. *Trichoderma*-plant root colonization: escaping early plant defense responses and activation of the antioxidant machinery for saline stress tolerance. *Plos Pathogens* 9(3): p.e1003221.

199. Zhang SW, Gan YT, Xu BL. 2016. Application of plant-growth-promoting fungi *Trichoderma longibrachiatum* T_6 enhances tolerance of wheat to salt stress through improvement of antioxidative defense system and gene expression. *Frontiers in Plant Science* 7: 1405.

200. Niu X, Song L, Xiao Y, Ge W. 201. Drought-tolerant plant growth-promoting rhizobacteria associated with foxtail millet in a semi-arid agroecosystem and their potential in alleviating drought stress. *Frontiers in Microbiology* 8.

201. Alfano G, Ivey MLL, Cakir C, Bos JIB, Miller SA, Madden LV, Kamoun S, Hoitink HAJ. 2007. Systemic modulation of gene expression in tomato by *Trichoderma hamatum* 382. *Phytopathology®* 97(4): 429-437.

202. Shoresh M, Harman GE, Mastouri F. 2010. Induced systemic resistance and plant responses to fungal biocontrol agents. *The* Annual Review *of* Phytopathology 48: 21-43 .

203. Mathys J, De Cremer K, Timmermans P, Van Kerckhove S, Lievens B, Vanhaecke M, Cammue BPA, De Coninck B. 2012. Genome-wide characterization of ISR induced in *Arabidopsis thaliana* by *Trichoderma hamatum* T382 against *Botrytis cinerea* Infection. *Frontiers in Plant Science* 3.

204. De Palma M, D'Agostino N, Proietti S, Bertini L, Lorito M, Ruocco M, Caruso C, Chiusano ML, Tucci M. 2016. Suppression Subtractive Hybridization analysis provides new insights into the tomato (*Solanum lycopersicum* L.) response to the plant probiotic microorganism *Trichoderma longibrachiatum* MK1. *Journal of Plant Physiology* 190: 79-94.

205. Pérez-Montano F, Alías-Villegas C, Bellogín RA, del Cerro P, Espuny MR, Jiménez-Guerrero I, López-Baena FJ, Ollero FJ, Cubo T. 2014. Plant growth promotion in cereal and leguminous agricultural important plants: From microorganism capacities to crop production. *Microbiological Research* 169: 325-336.

206. Ruocco M, Lanzuise S, Lombardi N, Woo SL, Vinale F, Marra R, Varlese R, Manganiello G, Pascale A, Scala V, Turrà D, Scala F, Lorito M. 2015. Multiple roles and effects of a novel *Trichoderma Hydrophobin*. *Molecular Plant-Microbe Interactions®* 28(2): 167-179.

207. Vos CM, De Cremer K, Cammue BP, De-Coninck B. 2015. The toolbox of *Trichoderma spp*. in the biocontrol of Botrytis cinerea disease. *Molecular Plant Pathology* 16: 400-412.

208. Lace B, Genre A, Woo S, Faccio A, Lorito M, Bonfante P. 2015. Gate crashing arbuscular mycorrhizas: *in vivo* imaging shows the extensive colonization of both symbionts by *Trichoderma atroviride*. *Environmental Microbiology Reports* 7(1): 64-77.

209. Contreras-Cornejo HA, Macias-Rodriguez L, Cortes-Penagos C, Lopez- Bucio J. 2009. *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in Arabidopsis. *Plant Physiology* 149: 1579-1592.

210. Howard BE, Hu Q, Babaoglu AC, Chandra M, Borghi M, Tan X, He L, Winter-Sederoff H, Gassmann W, Veronese P, Heber S. 2013. High-throughput RNA sequencing of pseudomonas-infected arabidopsis reveals hidden transcriptome complexity and novel splice variants. *Plos One* 8(10): p.e74183.

211. Zogli P, Libault M. 2017. Plant response to biotic stress: Is there a common epigenetic response during plant–pathogenic and symbiotic interactions? *Plant Science* 263: 89-93.

212. Sánchez-Blanco MJ, Ferrández T, Morales MA, Morte A, Alarcón JJ. 2004. Variations in water status, gas exchange, and growth in *Rosmarinus officinalis* plants infected with *Glomus deserticola* under drought conditions. *Journal of Plant Physiology* 161(6): 675-682.

213. Sánchez-Montesinos B, Diánez F, Moreno-Gavira A, Gea FJ, Santos M. 2019. Plant growth promotion and biocontrol of *Pythium ultimum* by saline tolerant *trichoderma* isolates under salinity stress. *International Journal of Environmental Research and Public Health* 16(11): 2053.

214. Chamala S, Feng G, Chavarro C, Barbazuk WB. 2015. Genome-wide identification of evolutionarily conserved alternative splicing events in flowering plants. *Frontiers in Bioengineering and Biotechnology* 3: 33.

215. Sharma A, Johri BN. 2003. Growth promoting influence of siderophore-producing *Pseudomonas* strains GRP3A and PRS9 in maize (*Zea mays* L.) under iron limiting conditions. *Microbiological Research* 158(3): 243-248.

216. Yang S, Vanderbeld B, Wan J, Huang Y. 2010. Narrowing down the targets: towards successful genetic engineering of drought-tolerant crops. *Molecular Plant* 3(3): 469-490.

217. Porcel R, Zamarreño Á, García-Mina J, Aroca R. 2014. Involvement of plant endogenous ABA in *Bacillus megaterium* PGPR activity in tomato plants. *BMC Plant Biology* 14(1): 36.

218. Ruzicka D. 2013. Inside arbuscular mycorrhizal roots - molecular probes to understand the symbiosis. *Plant Genome* 6: https://doi.org/10.3835/ plantgenome2012.06.0007.

219. Sun Y, Xiao H. 2015. Identification of alternative splicing events by RNA sequencing in early growth tomato fruits. *BMC Genomics* 16: 948.

220. Rodriguez RJ, Henson J, Van Volkenburgh E, Hoy M, Wright L, Beckwith F, Kim YO, Redman RS. 2008. Stress tolerance in plants via habitat-adapted symbiosis. *The ISME Journal* 2(4): 404-416.

221. Ahanger MA, Tyagi SR, Wani MR, Ahmad P. 2014. Drought Tolerance: Role of organic osmolytes, growth regulators, and mineral nutrients. physiological mechanisms and adaptation strategies in plants under changing environment. pp 25-55.

222. Sandham D. 2013. Thinking Cap. *Engineering AND Technology* 8(8): 100.

223. Zhu XC, Song FB, Xu HW. 2010. Arbuscular mycorrhizae improves low temperature stress in maize via alterations in host water status and photosynthesis. *Plant and Soil* 331(1/2): 129-137.

224. Sandhya V, SK ZA, Grover M, Reddy G, Venkateswarlu B. 2009. Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. *Biology and Fertility of Soils* 46(1): 17-26.

225. Bowles TM, Barrios-Masias FH, Carlisle EA, Cavagnaro TR, Jackson LE. 2016. Effects of arbuscular mycorrhizae on tomato yield, nutrient uptake, water relations, and soil carbon dynamics under deficit irrigation in field conditions. *Science of The Total Environment* pp 566-567.

226. Rouphael Y, Franken P, Schneider C, Schwarz D, Giovannetti M, Agnolucci M, Pascale SD, Bonini P, Colla G. 2015. Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. *Scientia Horticulturae* 196: 91-108.

227. Zou YN, Srivastava AK, Wu QS. 2016. Glomalin: A potential soil conditioner for perennial fruits. *Int. Journal of Agriculture and Biological Sciences* 18: 293-297.

228. Thirkell TJ, Charters MD, Elliott AJ, Sait SM, Field KJ. 2017. Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. *Journal of Ecology* 105(4): 921-929.

229. Paterson E, Sim A, Davidson J, Daniell TJ. 2016. Arbuscular mycorrhizal hyphae promote priming of native soil organic matter mineralization. *Plant and Soil* 408(1/2): 243-254.

230. Ahanger MA, Agarwal RM. 2017. Potassium up-regulates antioxidant metabolism and alleviates growth inhibition under water and osmotic stress in wheat (*Triticum aestivum* L). *Protoplasma* 254(4): 1471-1486.

231. Ahanger MA, Tittal M, Mir RA, Agarwal R. 2017. Alleviation of water and osmotic stress-induced changes in nitrogen metabolizing enzymes in *Triticum aestivum* L. cultivars by potassium. *Protoplasma* 254(5): 1953-1963.

232. Mena-Violante HG, Ocampo-Jimenez O, Dendooven L, Martinez-Soto G, Gonzalez-Castafeda J, Davies FT. 2006. Arbuscular mycorrhizal fungi enhance fruit growth and quality of chile ancho *Capsicum annuum* L. cv San Luis plants exposed to drought. *Mycorrhiza* 16: 261-267.

233. Sharma K, Gupta S, Thokchom SD, Jangir P, Kapoor R. 2021. Arbuscular mycorrhiza-mediated regulation of polyamines and aquaporins during abiotic stress: Deep insights on the recondite players. *Frontiers Plant Sciences* 12: 642101.

234. Yooyongwech S, Samphumphuang T, Tisarum R, Theerawitaya C, Chaum S. 2016. Arbuscular mycorrhizal fungi (AMF) improved water deficit tolerance in two different sweet potato genotypes involves osmotic adjustments via soluble sugar and free proline. *Scientia Horticulturae* 198: 107-117.

235. Moradtalab N, Hajiboland R, Aliasgharzad N, Hartmann TE, Neumann G. 2019. Silicon and the association with an Arbuscular-mycorrhizal fungus (*Rhizophagus clarus*) mitigate the adverse effects of drought stress on strawberry. *Agronomy* 9(1): 41.

236. Gianinazzi S, Gollotte A, Binet MN, Van Tuinen D, Redecker D, Wipf D. 2010. Agroecology: the key role of arbuscular mycorrhizas in ecosystem services. *Mycorrhiza* 20(8): 519-530.

237. Orfanoudakis M, Wheeler CT, Hooker JE. 2010. Both the arbuscular mycorrhizal fungus *Gigaspora rosea and Frankia* increase root system branching and reduce root hair frequency in *Alnus glutinosa*. *Mycorrhiza* 20(2): 117-126.

238. Gutjahr C, Paszkowski U. 2013. Multiple control levels of root system remodeling in arbuscular mycorrhizal symbiosis. *Frontiers in Plant Science* 4: 204.

239. Zhang X, Wang L, Ma F, Yang J, Su M. 2016. Effects of arbuscular mycorrhizal fungi inoculation on carbon and nitrogen distribution and grain yield and nutritional quality in rice (*Oryza sativa* L.). *Journal of the Science of Food and Agriculture* 97(9): 2919-2925.

240. Sheng M, Tang M, Chen H, Yang B, Zhang F, Huang Y. 2008. Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. *Mycorrhiza* 18: 287-296.

241. Ryals JA, Neuenschwander UH, Willits MG, Molina A, Steiner HY, Hunt MD. 1996. Systemic acquired resistance. The *Plant Cell*. 1809-1819.

242. Singh S, Parihar P, Singh R, Singh VP, Prasad SM. 2016. Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. *Front. Plant Sciences* 6: 1143.

243. Merlos MA, Zitka O, Vojtech A, Azcón-Aguilar C, Ferrol N. 2016. The arbuscular mycorrhizal fungus *Rhizophagus irregularis* differentially regulates the copper response of two maize cultivars differing in copper tolerance. *Plant Sciences* 253: 68-76.

244. Shah J, Zeier J. 2013. Long-distance communication and signal amplification in systemic acquired resistance. *Frontiers of Plant Science* 4: 1-16.

245. Jung HW, Tschaplinski TJ, Wang L, Glazebrook J, Greenberg JT. 2009. Priming in systemic plant immunity. *Science* 324(5923): 89-91.

246. Conrath U. 2009. Chapter 9 priming induced plant defense responses. *In*: Advances in Botanica 1 Research. Elsevier: Amsterdam. The Netherlands, 2009. pp 361-395.

247. Návarová H, Bernsdorff F, Döring AC, Zeier J. 2013. Pipecolic acid, an endogenous mediator of defense amplification and priming, is a critical regulator of inducible plant immunity. *Plant Cell* 24: 5123-5141.

248. Yi HS, Yang JW, Ryu CM. 2013. ISR meets SAR outside: additive action of the endophyte *Bacillus pumilus* INR7 and the chemical inducer, benzothiadiazole, on induced resistance against bacterial spot in field-grown pepper. *Frontiers in Plant Science* 4: 1-11.

249. Beckers GJM, Jaskiewicz M, Liu Y, Underwood WR, He SY, Zhang S, Conrath U. 2009. Mitogen-activated protein kinases 3 and 6 are required for full priming of stress responses in *Arabidopsis thaliana*. *Plant Cell* 21: 944-953.

250. Conrath U, Beckers GJM, Flors V, García-Agustín P, Jakab G, Mauch F, Newman MA, Pieterse CMJ, Poinssot B, Pozo MJ, Pugin A, Schaffrath U, Ton J, Wendehenne D, Zimmerli L, Mauch-Mani B. 2006. Priming: Getting ready for battle. *Molecular Plant-Microbe Interactions* 19(10): 1062-1071.

251. Madlung A, Comai L. 2004. The effect of stress on genome regulation and structure. *Annals of Botany* 94(4): 481-495.

252. Alagna F, Balestrini R, Chitarra W, Marsico AD, Nerva L. 2020. Getting ready with the priming Innovative weapons against biotic and abiotic crop enemies in a global changing scenario. Priming-Mediat. *Stress Cross-Stress Tolerance of Crop Plants* 2020: 35-56.

253. Lehman RM, Taheri WI, Osborne SL, Buyer JS, Douds DD. 2012. Fall cover cropping can increase arbuscular mycorrhizae in soils supporting intensive agricultural production. *Appl. Soil Ecology* 61: 300-304.

254. García-Garrido JM, Ocampo JA. 2002. Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. *Journal of Experimental Botany* 53(373):1377-1386.

255. Abd El-Daim IA, Bejai S, Meijer J. 2019. *Bacillus velezensis* 5113 Induced metabolic and molecular reprogramming during abiotic stress tolerance in wheat. *Scientific Reports* 9(1): https://doi.org/10.1038/s41598-019-52567-x.

256. Brahim AH, Jlidi M, Daoud L, Ben-Ali M, Akremi A, Hmani H, Feto NA, Ben-Ali M. 2019. Seed-Bio priming of durum wheat with diazotrophic plant browth promoting bacteria (PGPB) enhanced tolerance to *fusarium* head blight (FHB) and salinity stress. *Response Square* 12: 12.

257. Zubair, Hanif, Farzand, Sheikh, Khan, Suleman, Ayaz, Gao. 2019. Genetic screening and expression analysis of psychrophilic *Bacillus spp.* reveal their potential to alleviate cold stress and modulate phytohormones in wheat. *Microorganisms* 7(9): 337.