

Improving crop drought resistance with plant growth regulators and rhizobacteria: Mechanisms, applications, and perspectives

Hui Zhang, Xiaopeng Sun and Mingqiu Dai*

National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China

*Correspondence: Mingqiu Dai (mingqiudai@mail.hzau.edu.cn)

<https://doi.org/10.1016/j.xplc.2021.100228>

ABSTRACT

Drought is one of the main abiotic stresses that cause crop yield loss. Improving crop yield under drought stress is a major goal of crop breeding, as it is critical to food security. The mechanism of plant drought resistance has been well studied, and diverse drought resistance genes have been identified in recent years, but transferring this knowledge from the laboratory to field production remains a significant challenge. Recently, some new strategies have become research frontiers owing to their advantages of low cost, convenience, strong field operability, and/or environmental friendliness. Exogenous plant growth regulator (PGR) treatment and microbe-based plant biotechnology have been used to effectively improve crop drought tolerance and preserve yield under drought stress. However, our understanding of the mechanisms by which PGRs regulate plant drought resistance and of plant-microbiome interactions under drought is still incomplete. In this review, we summarize these two strategies reported in recent studies, focusing on the mechanisms by which these exogenous treatments regulate crop drought resistance. Finally, future challenges and directions in crop drought resistance breeding are discussed.

Key words: abiotic stress, drought tolerance, exogenous plant growth regulators, microbial, crops

Zhang H., Sun X., and Dai M. (2022). Improving crop drought resistance with plant growth regulators and rhizobacteria: Mechanisms, applications, and perspectives. *Plant Comm.* **3**, 100228.

INTRODUCTION

Abiotic stress negatively influences plant growth and development, leading to heavy losses in global agriculture (Verma, 2016). Drought contributes to the inhibition of crop growth and production. Because of global warming caused by human activities, people are confronted with a more parched and hotter planet. This situation is predicted to deteriorate in the next 30 years, and it is expected that over 50% of the regions on Earth will suffer from water scarcity in 2050 (Gupta et al., 2020a). Therefore, cultivation of drought-resistant crops to ensure food security is an urgent need.

In the process of evolution, plants have developed complex regulatory networks to cope with drought, including drought escape, drought avoidance, drought tolerance, and drought recovery after stress. Drought avoidance and drought tolerance are the main mechanisms for the improvement of plant drought resistance. “Drought avoidance” is the ability of a plant species to respond to drought by regulating morphological and physiological characteristics such as root growth, leaf structure, stomatal movement, photosynthesis, etc., in order to optimize water uptake and minimize water loss. “Drought tolerance”

refers to plant tolerance to moderate and severe drought by osmotic adjustment and an antioxidant defense system to maintain cell turgor and scavenge harmful substances (Ludlow et al., 1989). The mechanism of plant drought resistance has been well studied in recent years, and diverse drought resistance genes have been identified (Liu et al., 2013a; Mao et al., 2015; Wang et al., 2016; Xiang et al., 2017; He et al., 2018, 2019; Zhang et al., 2020a, 2020b), but transferring this knowledge into crops with enhanced stress resistance remains challenging (Tardieu, 2012; Zhu, 2016). Among major crops, only one transgenic maize cultivar with a drought resistance trait has been commercialized to date (Castiglioni et al., 2008). In addition, the use of chemical fertilizers in agriculture has caused heavy energy losses and significant damage to the environment (Guo et al., 2010; White and Brown., 2010; Liu et al., 2013b). Therefore, effective and environmentally friendly new strategies for improving crop drought resistance are urgently needed.

Published by the Plant Communications Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

Recently, a variety of new strategies have been devised to improve plant performance under environmental stress. Numerous studies have indicated that exogenous application of various PGRs, such as hormones, hormone agonists, polyamines (PAs), nutrients, antioxidants, osmoprotectants, and others, enhances crop drought tolerance (Raza et al., 2012; Latif et al., 2016; Vaidya et al., 2019; Hassan et al., 2020; Huan et al., 2020; Veroneze-Júnior et al., 2020). According to these studies, the application of such compounds can enhance parameters such as morphology, photosynthetic capacity, relative water content (RWC), and gas exchange attributes. Furthermore, the application of these compounds also promotes the accumulation of osmolytes and antioxidants to maintain osmotic balance and scavenge reactive oxygen species (ROS), thereby ensuring the stability of membrane structures, enzymes, and other macromolecules under drought stress. Such priming treatment is a very promising strategy in modern crop production management, as it enables plants to respond to abiotic stress faster and more strongly (Xiao et al., 2017).

It has also been demonstrated that microbe-based plant biotechnology is an alternative strategy for effectively improving plant drought resistance (Naseem et al., 2018). The rhizosphere is a natural ecosystem that hosts various kinds of microbes, including bacteria, actinobacteria, fungi, algae, and protozoa (Mendes et al., 2013; Rout and Southworth, 2013). Plants and the rhizosphere microbiome interact through several distinct mechanisms. Plants fuel the soil food web through their belowground carbon (C) inputs. In turn, the activities of the rhizosphere microbiome release nutrients for plant growth and determine the balance between C respiration and stabilization in the soil. In addition, the microbiome interacts directly with plants in the rhizosphere by feeding on (or infecting) roots, forming symbiotic relationships, or promoting plant growth through phytohormone production or the reduction of plant stress signaling (de Vries et al., 2020). However, despite an increasing understanding of plant-microbiome interaction mechanisms, our understanding of these mechanisms under drought is quite limited.

Over the past few years, the use of exogenous PGRs and microbe-based plant biotechnology to enhance crop drought resistance has become pioneering research because of their better field operability and environmental friendliness. In this review, we summarize studies of exogenous PGR application and microbial inoculation that aimed to improve crop drought resistance, focusing on the mechanisms by which these exogenous treatments regulate crop drought resistance. Finally, we propose and discuss future challenges and directions in crop drought resistance breeding.

ROLES OF EXOGENOUS PLANT GROWTH REGULATORS IN DROUGHT RESISTANCE

In recent years, a large number of studies have demonstrated that application of exogenous PGRs by seed priming, root irrigation, or foliar spraying is an effective strategy to improve drought resistance by: (1) improving plant antioxidant capacity, (2) promoting plant osmotic adjustment capacity, (3) protecting the photosynthetic system and maintaining plant photosynthetic efficiency,

(4) changing the external and internal structure of roots and leaves to improve water absorption and transport, (5) regulating the processes of nutrient and energy metabolism, and (6) regulating the expression of functional genes and the activities of functional proteins (Table 1). In this review, exogenous PGRs are classified into hormones, PAs, nutrients, amino acids, sugars, and others in order to discuss their specific roles in the regulation of plant drought resistance.

Hormones

Abscisic acid (ABA) plays a vital role in drought response. A series of studies have shown that exogenous ABA treatment is an effective way to improve plant drought resistance. For example, exogenous ABA treatment can regulate the processes of energy metabolism, amino acid metabolism, and lipid metabolism; promote the accumulation of flavonoids, betaine, and other substances; improve enzymatic and non-enzymatic antioxidant regulation systems; and enhance the photosynthetic performance and RWC of plants to promote plant growth and improve drought resistance of a diversity of crops, including maize, wheat, sweet potato, pearl millet, and other plants (Zhang et al., 2012; Wei et al., 2015; Awan et al., 2020; Huan et al., 2020). In addition, spraying leaves with 2 mg/l 1',4'-*trans*-diol-ABA, a key precursor of ABA biosynthesis in fungi, enhanced the drought tolerance of tobacco seedlings by upregulating many transcription factors and some key regulators in the ABA signaling pathway (Liu et al., 2021). Some studies have shown that treatment with ABA and jasmonate or benzylaminopurine simultaneously is more effective in promoting plant drought resistance (Awan et al., 2020; Huan et al., 2020).

Although ABA can be used directly as an agrochemical, its use has been limited by its rapid conversion into biologically inactive metabolites (Gupta et al., 2020b). Therefore, to overcome the limitations of ABA use in various agricultural applications, several types of ABA-mimicking agents have been developed. Pyrabactin was the first synthetic ABA agonist discovered; it displays several ABA-like activities, such as inhibition of seed germination, induction of stomatal closure, and enhancement of root hydraulic conductivity (Park et al., 2009; Puli and Raghavendra, 2012; Fan et al., 2015). In 2013, the dihydroquinolinone-sulphonamide analog quinabactin (also known as ABA mimic 1 [AM1]) was identified by two separate teams as a potential ABA-mimicking agent that exhibited nine- and eight-fold better agonist activities than ABA and pyrabactin, respectively. According to Cao et al. (2013) and Okamoto et al. (2013), quinabactin induced a range of ABA-like biological responses, including inhibition of seed germination, control of leaf water loss, and enhancement of drought tolerance in *Arabidopsis* and soybean. The structural optimization of quinabactin led to the identification of AM1 fluorine derivatives (AMFs) that exhibited more pronounced agonist activities than the parent compound quinabactin. The AMF ABA analogs displayed long-lasting effects on the promotion of stomatal closure and the induction of stress-responsive gene expression (Cao et al., 2017). Recently, Vaidya et al. (2019) combined virtual screening, X-ray crystallography, and structure-guided design to develop opabactin (OP), an ABA mimic with up to an approximately seven-fold increase in receptor affinity relative to ABA and up to 10-fold greater activity *in vivo*. They demonstrated that OP has activities in multiple monocots and eudicots and addressed the

PGRs		Crops	Mechanism	References
Hormones	ABA	maize (<i>Zea mays</i> L.)	enhanced glycinebetaine (GB) accumulation, modulated water relations and plant growth, increased the levels of Glutathione (GSH) and AsA	Zhang et al. (2012)
		wheat (<i>Triticum aestivum</i> L.)		Wei et al. (2015)
	ABA/JA	pearl millet (<i>Pennisetum glaucum</i> L.)	Improved the capacities of antioxidant enzymes	Awan et al. (2020)
	ABA/6-BA	sweet potato (<i>Ipomoea batatas</i>)	increased the endogenous hormone contents, enhanced carbon metabolism enzyme activities, improved photosynthesis, and regulated the source-sink balance	Huan et al. (2020)
	AsA	chickpea (<i>Cicer arietinum</i> L.)	enhanced antioxidant capacity	Hussain et al. (2020)
	Melatonin	maize (<i>Zea mays</i> L.)	maintained growth, enhanced root vigor and leaf cuticle formation, improved photosynthetic characteristics, promoted aquaporin activity, increased water uptake and transport, and improved capacities of antioxidant enzymes, regulated the carbohydrate balance to improved male fertility	Ahmad et al. (2019); Huang et al. (2019); Qiao et al. (2020)
		soybean (<i>Glycine max</i>)		Zhang et al. (2019a, 2019b); Zhang et al. (2020c)
		tomato (<i>Solanum lycopersicum</i> L.)		Liu et al. (2015); Ding et al. (2018)
		cotton (<i>Gossypium hirsutum</i> L.)		Hu et al. (2020)
	SA	barley (<i>Hordeum vulgare</i> L.)	maintained photosynthesis, enhanced antioxidant defense abilities and energy metabolism	Habibi (2012)
		wheat (<i>Triticum aestivum</i> L.)		Sharma et al. (2017)
	SA/MeJA	maize (<i>Zea mays</i> L.)	increased osmolytes and endogenous ABA accumulation, improved capacities of antioxidant enzymes	Tayyab et al. (2020)
ABA agonists	AMFs	soybean (<i>Glycine max</i>)	activated ABA signaling, promoted stomatal closure, and induced the expression of stress-responsive genes	Cao et al. (2017)
	OP	tomato (<i>Solanum lycopersicum</i> L.)/ wheat (<i>Triticum aestivum</i> L.)	activated ABA signaling, decreased the blade surface temperature	Vaidya et al. (2019)
	pyrabactin	pea (<i>Pisum sativum</i> L.)	induced stomatal closure, improved root hydraulic properties	Puli and Raghavendra (2012)
		maize (<i>Zea mays</i> L.)		Fan et al. (2015)
	quinabactin	soybean (<i>Glycine max</i>)	activated ABA signaling, induced stomatal closure	Okamoto et al. (2013)
Polyamines (Spd/Put/Spm)Polyamines (Spd/Put/Spm)		maize (<i>Zea mays</i> L.)	protected mesophyll cells structurally and functionally, changed endogenous PAs and phytohormones, improved photosynthesis, water-use efficiency,	Li et al. (2018a)
		rice (<i>Oryza sativa</i> L.)		Farooq et al. (2009)
		barley (<i>Hordeum vulgare</i> L.)		Kubiś, 2005

Table 1. Roles and mechanisms of PGRs in crop drought tolerance.

(Continued on next page)

PGRs		Crops	Mechanism	References
		wheat (<i>Triticum aestivum</i> L.)	leaf water status, osmoregulation, and antioxidant defense system	Gupta et al. (2012); Liu et al. (2016); Ebeed et al. (2017); Doneva et al. (2021); Hassan et al. (2020); Marcińska et al. (2020)
Nutrients	K	wheat (<i>Triticum aestivum</i> L.)	improved growth and yield components	Raza et al. (2012)
	N	wheat (<i>Triticum aestivum</i> L.)	improved growth and root development	Gevrek and Atasoy (2012)
	N/P/K	wheat (<i>Triticum aestivum</i> L.)	improved water relations, gas-exchange characteristics and nutrient contents, improved growth, increased osmolyte accumulation and improved antioxidant machinery	Shabbir et al. (2015); 2016
	Se	maize (<i>Zea mays</i> L.)	maintained plant growth, enhanced relative water contents and total chlorophyll, upregulated osmotic adjustment and antioxidant defense system, activated the expression of <i>PSY</i> , <i>SDH</i> , and <i>ADH</i> gene	Nawaz et al. (2013, 2014, 2015, 2016); Bocchini et al. (2018)
	Si	rice (<i>Oryza sativa</i> L.)	enhancement of photochemical efficiency and adjustment of the mineral nutrient absorption and phytohormone levels	Chen et al. (2011)
		wheat (<i>Triticum aestivum</i> L.)		Xu et al. (2017)
	urea/NBPT	maize (<i>Zea mays</i> L.)	protected photosynthetic apparatus, improved osmotic adjustment and antioxidant defense system	Gou et al. (2017)
Amino acid	Zn	maize (<i>Zea mays</i> L.)	enhanced parameters including morphology, chlorophyll contents, RWC, gas-exchange attributes, activities of antioxidant enzymes, and the content of proline and soluble sugar	Shemi et al. (2021)
	Arg	wheat (<i>Triticum aestivum</i> L.)	upgraded water status and reduced oxidative stress and methyl-glyoxal (MG) toxicity	Hasanuzzaman et al. (2018)
	BABA	faba bean (<i>Vicia faba</i> L.)	improved the osmotic adjustment and antioxidant defense ability, changes in endogenous ABA and JA concentrations, regulated the expression of drought tolerance-related genes	Abid et al. (2020)
		maize (<i>Zea mays</i> L.)		Shaw et al. (2016)

Table 1. Continued

(Continued on next page)

PGRs		Crops	Mechanism	References
	GABA	snap bean (<i>Phaseolus vulgaris</i> L.)	improvement in growth, water status, membrane integrity, osmotic adjustment, antioxidant defense, and nutrient acquisition	Abd El-Gawad et al., 2021
	L-ornithine	sugar beet (<i>Beta vulgaris</i> var. <i>saccharifera</i> L.)	improved osmotic adjustment and antioxidant defense system	Hussein et al. (2019)
	Pro	oats (<i>Avena sativa</i> L.)	enhanced leaf mesophyll thickness and metaxylem area, suppressed leaf midrib thickness and phloem area, increased proline and total soluble protein contents, improved photosynthesis, growth, seed oil quality, and enhanced seed oil 1,1-diphenyl-2-picryl-hydrazyl (DPPH) free radical-scavenging activity	Ghafoor et al. (2019)
		maize (<i>Zea mays</i> L.)		Ali et al. (2007); 2013
	5-ALA	sunflower (<i>Helianthus annuus</i> L.)	modulated growth, secondary metabolism, and antioxidant defense	Rasheed et al. (2020)
Sugars	Chitosan	potato (<i>Solanum tuberosum</i> L.)	improved relative tissue water content, photosynthesis and stomatal conductance, osmoregulation, and antioxidant defense system	Jiao et al. (2012)
		sugarcane (<i>Saccharum</i> spp.)		Mirajkar et al. (2019)
		sunflower (<i>Helianthus annuus</i> L.)		Shehzad et al. (2020)
		maize (<i>Zea mays</i> L.)		Veroneze-Júnior et al. (2020)
	Trehalose	sunflower (<i>Helianthus annuus</i> L.)	improved photosynthesis, plant growth, yield, seed quality, and antioxidant defense system	Kosar et al. (2020)
		maize (<i>Zea mays</i> L.)		Ali and Ashraf. (2011)
Others	ALA	maize (<i>Zea mays</i> L.)	induced photosystem II activity and the gene expressions of carbon fixation and chlorophyll metabolism enzymes	Sezgin et al. (2019)
	AsA	cauliflower (<i>Brassica oleracea</i> L.)	improved osmoregulation and the enzymatic and non-enzymatic antioxidant defense systems	Latif et al. (2016)
	BBS	wheat (<i>Triticum aestivum</i> L.)	improved the enzymatic and non-enzymatic antioxidant defense systems	Elkeilsh et al. (2019)
	DCPTA	maize (<i>Zea mays</i> L.)	improved N metabolism	Xie et al. (2019)
	GlyBet	sweet potato (<i>Ipomoea batatas</i>)	maintained osmotic potential	Tisarum et al. (2020)
	H ₂ O ₂	rice (<i>Oryza sativa</i> L.)	induced amylase activity under drought stress	Wang et al. (2018)
	NO/GSNO	sugarcane (<i>Saccharum</i> spp.)	protected the photosynthetic apparatus and improved shoot and root growth	Silveira et al. (2016)

Table 1. Continued

(Continued on next page)

PGRs	Crops	Mechanism	References
PopW	tomato (<i>Solanum lycopersicum</i> L.)	enhanced water-retention capacity, balanced redox homeostasis, increased osmotic adjustment, reduced membrane damage, and decreased stomatal aperture	Tisarum et al. (2020)
1',4'-trans-diol-ABA	tobacco (<i>Nicotiana tabacum</i> L.)	upregulated bZIP, ERF, MYB, NAC, WRKY, and HSF transcription factor families and the levels of expression of PYL/PYR, PP2C, SnRK2, and ABF	Liu et al. (2021)
βCC	tomato (<i>Solanum lycopersicum</i> L.)	increased photosynthesis, enhanced root growth, enhanced proline accumulation and activity of SOD	Deshpande et al. (2020)

Table 1. Continued

PGR abbreviations: 1',4'-trans-diol-ABA, a key precursor of the biosynthesis of ABA; 5-ALA, 5-aminolevulinic acid; N-Acetyl-5-methoxytryptamine, melatonin; ABA, abscisic acid; ALA α-lipoic acid; 5-ALA, 5-aminolevulinic acid; Arg, L-arginine; AsA, ascorbic acid; 6-BA, benzylaminopurine; BABA, β-aminobutyric acid; βCC, β-cyclocitral; BBS, β-sitosterol; DCPTA, 2-(3,4-dichlorophenoxy) trimethylamine; GABA, γ-aminobutyric acid; GlyBet, glycine betaine; GSNO, nitric oxide/S-nitrosoglutathione; H₂O₂, hydrogen peroxide; K, potassium; MeJA, methyl jasmonate; N, nitrogen; NBPT, urease inhibitor N-(n-butyl) thiophosphoric triamide; PopW, a harpin protein; Pro, proline; SA, salicylic acid; Se, selenium; Si silicon; Zn, zinc.

limitations of existing sulfonamide molecules. OP functions as an antitranspirant to enhance drought tolerance and hyperactivates ABA transcriptional responses in wheat. All these studies indicate that synthetic ABA agonists have great application prospects for the mitigation of drought impacts on crop yields.

Salicylic acid (SA) is another plant hormone that regulates plant growth and abiotic stress responses. Proteomic data from wheat plants treated with exogenous SA and drought showed that the differentially expressed proteins induced by exogenous SA under drought stress were involved in the regulation of photosynthesis, carbon assimilation, protein metabolism, amino acid metabolism, energy metabolism, redox balance, signal transduction, and other biological processes, suggesting that SA may regulate these physiological processes to enhance wheat drought resistance (Sharma et al., 2017). In addition, Hussain et al. (2020) suggested that the application of acetylsalicylic acid (a derivative of SA) also improved the drought resistance of chickpea by activating the antioxidant defense system. As the main representative jasmonate substances, jasmonic acid (JA) and methyl jasmonate (MeJA) are also endogenous PGRs in higher plants. The combined application of SA and MeJA has been shown to promote the accumulation of endogenous ABA and osmotic adjustment substances and to improve the activities of antioxidant enzymes, thereby improving maize drought resistance (Tayyab et al., 2020).

Melatonin is an evolutionarily conserved pleiotropic molecule that exists ubiquitously in living organisms and has rich biological functions (Hardeland, 2015; Debnath et al., 2019). In the last few years, the role of melatonin in plants has been studied progressively. A series of studies have shown that exogenous melatonin application by foliar spraying, root irrigation, or seed pretreatment effectively improves the drought resistance of maize, soybean, cotton, and tomato by boosting their growth, photosynthesis, and antioxidant activities (Liu et al., 2015; Ding et al., 2018; Ahmad et al., 2019; Huang et al., 2019; Zhang et al., 2019a, 2019b, 2020c; Hu et al., 2020; Qiao et al., 2020). The physiological and molecular activities of melatonin in plants indicate that it is an essential molecule in the stimulation of field crops, especially under abiotic stress.

PAs

PAs are low-molecular-weight aliphatic polycations that exist in all living organisms and are considered to be a new class of PGRs. PAs are widely involved in many physiological and biochemical processes, including seed germination, root development, plant architecture formation, *in vitro* plant regeneration, flowering, senescence, photosynthesis, membrane stability, enzyme activation, ion transport, hormone activity, cell death, DNA synthesis, gene transcription, protein translation, and chromatin organization (Moschou and Roubelakis-Angelakis, 2014; Tian et al., 2018; Igarashi and Kashiwagi, 2019). There are three major PAs in plants: putrescine, spermidine, and spermine. Endogenous plant PA levels were induced by abiotic stress (Alcázar et al., 2020). Treatment with spermidine regulated endogenous PA levels and plant hormones, effectively improving the antioxidant capacity of plants under drought stress (Kubiś, 2005; Li et al., 2018a). Gupta et al. (2012) and Doneva et al. (2021) reported that exogenous putrescine treatment promoted the accumulation of proline, soluble sugars, and other osmotic adjustment substances in

wheat plants under drought stress and improved their antioxidant capacity and photosynthesis. In addition, some studies have explored the cooperative effects of different PAs on plant drought resistance. For example, combined treatment with two or three exogenous PAs effectively enhanced the drought resistance of rice and wheat (Farooq et al., 2009; Liu et al., 2016; Ebeed et al., 2017; Hassan et al., 2020; Marcińska et al., 2020). Compelling evidence thus indicates that PAs have a protective role against drought stress in different plant species.

Amino acids

Proline exists widely in higher plants and plays roles in drought response mainly through the mechanism of osmotic adjustment. Ali et al. (2007, 2013) revealed that foliar spraying of maize seedlings with proline effectively promoted the growth of maize plants by improving photosynthesis and increasing antioxidant compounds. In addition to proline, other amino acids can also improve plant drought resistance. For example, spraying L-ornithine improved the drought resistance of sugar beet (Hussein et al., 2019). Treatment of roots with arginine and the nitric oxide (NO) donor sodium nitroprusside improved the drought resistance of wheat (Hasanuzzaman et al., 2018).

In addition, some non-protein-coding amino acids also play roles in crop drought resistance. γ -aminobutyric acid and β -aminobutyric acid are induced under abiotic stress and improve plant drought resistance via mechanisms including promotion of endogenous ABA and JA accumulation, regulation of drought stress-related gene expression in leaves and roots, induction of stomatal closure, and improvement of osmotic adjustment ability and antioxidant capacity (Shaw et al., 2016; Abid et al., 2020; Abd El-Gawad et al., 2021). 5-aminolevulinic acid (5-ALA) is an essential precursor of chlorophyll molecule biosynthesis. Rasheed et al. (2020) showed that 5-ALA-mediated stress tolerance is related to lower cellular levels of ROS (H_2O_2), decreased lipid peroxidation (malondialdehyde (MDA) content), and reduced degradation of photosynthetic pigments.

Nutrients

Nitrogen (N), phosphorus (P), and potassium (K) are essential plant macronutrients that are normally applied in the form of chemical fertilizer in agricultural production to promote crop growth and yield. However, drought reduces the capacity of plants to absorb nutrients from the soil. Foliar spraying of N, P, or K alone or in combination can effectively alleviate the negative effects of drought stress on wheat growth and production (Raza et al., 2012; Gevrek and Atasoy, 2012; Shabbir et al., 2015, 2016). According to Gou et al. (2017), spraying urea (N source) and urease inhibitor on maize leaves can also effectively increase dry weight and photosynthetic pigment content, improve RWC, promote the accumulation of osmotic adjustment substances such as proline and soluble sugars, and improve the activities of antioxidant enzymes such as catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD).

In addition, some studies have shown that exogenous application of selenium (Se), silicon (Si), and zinc (Zn) can also effectively improve plant drought resistance. For example, exogenous Se has been applied to wheat by soaking seeds, fertilization, or foliar spraying, thereby maintaining wheat growth under drought stress

and enhancing the production of osmolytes and antioxidant enzymes (Nawaz et al., 2013, 2014, 2015). Bocchini et al. (2018) found that Se treatment activates several genes that belong to special classes and are involved in tolerance to abiotic stress; these include *phytoene synthase* (PSY), essential for maintaining leaf carotenoid content, *sorbitol dehydrogenase* (SDH), whose activity regulates the level of important osmolytes during drought stress, and *alcohol dehydrogenase* (ADH), whose activity plays a central role in biochemical adaptation to environmental stress. Si helps plants to resist high salt and drought stress (Zhu and Gong, 2013). Exogenous Si treatment effectively enhanced photosynthetic efficiency and modulated nutrient uptake (K, Na, CA, Mg, Fe, Si) and endogenous plant hormone levels (ABA, indole-3-acetic acid [IAA], JA), thereby promoting plant growth under drought stress (Chen et al., 2011; Xu et al., 2017). Zn is another essential micronutrient that plays critical roles in drought resistance by detoxifying ROS and increasing antioxidant enzymes (Sofy, 2015). According to Shemi et al. (2021), the application of Zn to maize leaves enhanced parameters such as morphology, chlorophyll contents, RWC, gas exchange attributes, activities of antioxidant enzymes, and levels of proline and soluble sugars under drought stress. The aforementioned studies show that exogenous application of nutrients improved crop drought resistance not only by promoting nutrient metabolism and growth but also by regulating various physiological processes under drought stress.

Sugars

As one of the main osmotic adjustment substances, trehalose plays an important role in plant drought stress response (Lunn et al., 2014). Specifically, it acts as a signal molecule and antioxidant in plant stress responses (Iturriaga et al., 2009). For instance, Joshi et al. (2020) found that overexpression of trehalose synthase effectively improved rice drought resistance. Exogenous trehalose treatment has also been reported to effectively improve photosynthetic efficiency and water usage in maize, promote the growth and yield of sunflower, and activate the antioxidant defense system of crops (Ali and Ashraf, 2011; Kosar et al., 2020). Chitosan is another type of polysaccharide reported to effectively enhance plant drought resistance. For example, exogenous chitosan treatment promoted plant growth, photosynthetic efficiency, osmotic adjustment, and antioxidant capacity, ultimately improving yield under drought stress in various crops, including sunflower, maize, potato, and sugarcane (Jiao et al., 2012; Mirajkar et al., 2019; Shehzad et al., 2020; Veroneze-Júnior et al., 2020).

Others

In addition to the aforementioned PGRs, many other PGRs have been found to function in plant drought resistance (Table 1). For example, spraying maize leaves with the new PGR DCPTA regulated the N metabolism process of maize under drought stress and improved maize drought resistance at the early flowering stage (Xie et al., 2019). Sezgin et al. (2019) reported that exogenous α -lipoic acid (ALA) improved the photosynthetic performance of maize seedlings exposed to drought by inducing the expression of genes encoding carbon (C) fixation and chlorophyll metabolism enzymes such as *ribulose-1,5-bisphosphate carboxylase* (Rubisco), *phosphoenolpyruvate carboxylase* (PEPc), *Rubisco activase* (RCA), *chlorophyll*

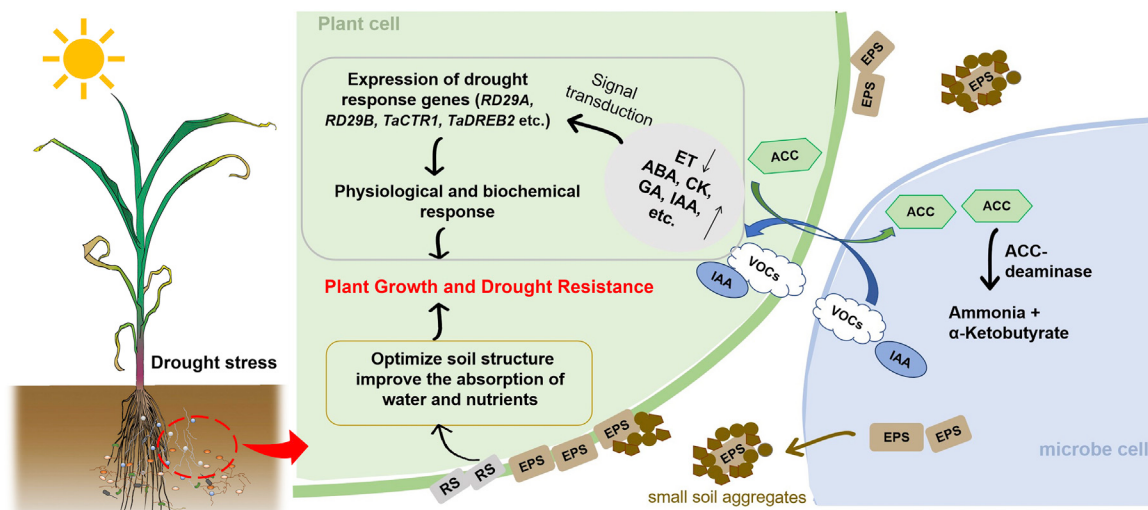


Figure 1. Mechanistic pathway for PGPR-mediated drought tolerance in plants.

Main mechanisms of PGPR-mediated plant drought resistance.

- (1) PGPRs regulate the accumulation of abscisic acid (ABA), auxin (IAA), cytokinin (CK), and gibberellin (GA) in plant cells to activate signal transduction pathways.
- (2) PGPRs produce ACC deaminase to reduce ethylene (ET) content in roots, activating signal transduction pathways.
- (3) PGPRs produce exopolysaccharide (EPS) to form EPS biofilms, rhizosheath structures (RS), and small soil aggregates, helping plants to absorb water and nutrients under drought stress.
- (4) PGPRs produce volatile organic compounds (VOCs) under drought stress, activating plant drought response without direct plant contact.

metabolism magnesium chelatase (*MgChlH*), and chlorophyllase (*Chlase*) and by increasing Rubisco LSU protein content (Sezgin et al., 2019). H_2O_2 is an ROS that plays a dual role in plant cells. In rice aleurone layers, exogenous H_2O_2 (as a signaling molecule) triggered heme oxygenase-1 (HO-1, EC.1.14.99.3) and delayed programmed cell death via cyclic guanosine monophosphate, which possibly induced amylase activity under drought stress (Wang et al., 2018). In addition, β -cyclocitral (the main oxidation product of β -carotene), β -sitosterol, ascorbic acid, GSNO (the main NO reservoir in cells), NO, glycine betaine, and PopW (a hairpin protein from *Ralstonia solanacearum* ZJ3721) have been shown to maintain plant photosynthesis and RWC and to promote osmotic adjustment and antioxidant defense, thereby enhancing plant drought resistance (Latif et al., 2016; Silveira et al., 2016; Elkeilsh et al., 2019; Deshpande et al., 2020; Rasheed et al., 2020; Tisarum et al., 2020; Zhou et al., 2020). Based on the aforementioned studies, we found that a large number of synthetic compounds that effectively improve plant drought resistance are osmoprotectants or antioxidants. Although exogenous PGRs can enhance crop drought resistance through various physiological mechanisms, the two main mechanisms are improvements in osmoregulation and the antioxidant defense system of crops. This conclusion provides guidance and experience for the screening of effective compounds to improve crop drought resistance.

IMPROVING DROUGHT RESISTANCE BY MICROBIAL INOCULATION

Under abiotic stress, different changes and enrichment in rhizosphere communities are associated with changes in plant metabolites (Santos-Medellin et al., 2017). Many previous studies have

shown that plant root microbes are associated with the drought resistance of host plants (Walters et al., 2018; Xu et al., 2018; Zhang et al., 2019a, 2019b). Plant growth-promoting rhizobacteria (PGPR) are a type of bacteria that live in the rhizosphere or as epiphytes in roots and have positive effects on the growth, nutrient uptake, and systemic stress resistance of their host plants (Vurukonda et al., 2016). Studies have revealed three main mechanisms of PGPR-mediated plant drought resistance (Figure 1): (1) synthesis of PGRs such as ABA, gibberellin (GA), and IAA; (2) production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase to reduce ethylene content in roots; (3) production of exopolysaccharide (EPS) (Lakshmanan et al., 2017). In addition, some volatile organic compounds (VOCs) produced by PGPR secondary metabolism may regulate plant growth without inoculation or physical contact with plants (Cappellari et al., 2017; Rojas-Solis et al., 2018; Hashem et al., 2019).

Effects of PGPRs on PGR levels in plants under drought stress

Under drought stress, PGPRs regulate the accumulation of PGRs in plant cells, and this is one of the main mechanisms by which root microbes promote plant drought resistance (Arvin et al., 2012; Spence et al., 2014; Lakshmanan et al., 2017). Cohen et al. (2009) reported that inoculation of maize with the endophyte *Azospirillum lipoferum* enhanced the production of ABA, IAA, and GA in host plants and further improved plant drought resistance. IAA exists in both plants and microbes and plays important roles in the regulation of root development. Studies have shown that *Bacillus thuringiensis* and *Azospirillum* can synthesize IAA to promote the growth of lateral roots and root hairs in host plants, contributing to improved water absorption capacity and drought resistance (Arzanesh et al.,

2011; Armada et al., 2014). In addition, endophytes can promote root growth and reduce yield loss under drought conditions. For example, inoculation of wheat and maize plants with *Pantoea alhagi* or *Burkholderia phytofirmans* improved plant growth, root length, and drought resistance (Naveed et al., 2014; Chen et al., 2017). Liu et al. (2018) reported that arbuscular mycorrhizal fungi upregulated the expression of IAA biosynthesis genes and downregulated the expression of genes encoding outward IAA transporters in roots, thus improving IAA levels in roots, enhancing the growth of root hairs, and promoting plant drought resistance.

Effect of ACC deaminase-containing PGPRs on plant drought resistance

Ethylene, a plant hormone, is important for the normal growth and development of plants, and drought stress results in ethylene accumulation. Under stress, most plants secrete the ethylene synthesis precursor ACC as a root exudate. High levels of ethylene accumulation inhibit growth and development and may even lead to plant death (Iqbal et al., 2017). ACC deaminase can degrade ACC into amines and ketobutyric acid, thereby reducing ethylene accumulation under drought stress, and this is one of the main mechanisms of PGPR-mediated plant drought resistance (Volpe et al., 2018). Studies have shown that inoculation of tomato and pepper with *Achromobacter* ARV8, a PGPR that produces ACC deaminase, reduces ethylene levels and improves drought resistance of host plants (Mayak et al., 2004). In addition, inoculation with ACC deaminase-producing PGPRs has positive effects on photosynthetic efficiency, stomatal conductance, water-use efficiency, transpiration rate, vapor pressure, chlorophyll content, and carbon content of maize plants under drought stress (Danish et al., 2020; Nadeem et al., 2020). ACC deaminase-producing PGPRs also enhance osmotic adjustment and antioxidant defenses of host plants under drought stress (Gowtham et al., 2020; Zarei et al., 2020).

Effect of EPS-producing PGPRs on plant drought resistance

EPS is a polysaccharide macromolecule with high water-holding capacity produced by rhizobacteria (Roberson and Firestone, 1992). The EPS-producing bacteria *Pseudomonas putida* GAP-P45 can form a biofilm on the root surface, and plants inoculated with this strain show greater soil aggregation, more root-adhering soil, and high leaf RWC (Sandhya et al., 2009). Nadeem et al. (2020) found that EPS-producing bacteria improved the photosynthetic rate, stomatal conductance, and other physiological characteristics of maize under drought stress. Studies showed that the integrated use of ACC deaminase-producing bacteria and EPS-producing bacteria had more beneficial effects on plant drought resistance than the use of either bacteria separately (Nadeem et al., 2020). Soil structure is very important for crop production. Drought stress can change the biochemical and physicochemical properties of soil, making it unsuitable for the growth of crops and bacteria (Bais et al., 2006; Berg and Smalla, 2009). EPS-producing bacteria are conducive to the formation of small soil aggregates, which are important for the maintenance of soil structure and health (Wezel et al., 2014). Inoculation with EPS-producing bacteria optimized soil structure, increased root adhering soil per unit root tissue, and

further improved plant drought resistance (Alami et al., 2000; Sandhya et al., 2009). EPS is also conducive to the formation of rhizosheath structures on plant roots, which aid the absorption of nutrients and water (Roessner et al., 2001; Kohler et al., 2008; Wezel et al., 2014). In addition, EPS-producing bacteria have been shown to participate in the regulation of osmotic adjustment and the antioxidant defense system. We may conclude that PGPR application in combination with EPS is a promising measure for combatting drought stress and thereby increasing global food security.

PGPRs generate VOCs and regulate drought-responsive gene expression

VOCs are products emitted into the atmosphere from natural sources (Holopainen and Gershenzon, 2010). Some VOCs produced by PGPRs can regulate plant growth without inoculation or physical contact with plants (Cappellari et al., 2017; Rojas-Solis et al., 2018; Hashem et al., 2019), and this is another effective way for PGPRs to improve plant drought resistance. These VOCs stimulated numerous signal transduction pathways in plants to initiate a cascade of complex metabolic reactions, which not only alleviated symptoms caused by stress but also enhanced plant growth (Schulz-Bohm et al., 2018). Yasmin et al. (2020) reported that VOCs of *Pseudomonas pseudoalcaligenes* induced systemic resistance in maize under drought stress. The VOC-exposed maize increased its drought resistance by reducing electrolyte leakage and MDA accumulation, enhancing chlorophyll and proline biosynthesis, and activating antioxidant enzymes in shoots and roots.

As mentioned above, microbes can promote plant drought resistance by regulating the accumulation of ABA, IAA, cytokinin, GA, ethylene, or other signaling molecules in plant cells, activating downstream signal transduction pathways and thereby controlling a series of physiological and biochemical responses. Drought stress causes changes in the expression of various stress-responsive genes at the transcriptional level. Wang et al. (2005) found that the endophytic bacteria *Pseudomonas fluorescens* upregulated the expression of 105 genes in *Arabidopsis*, and this was positively correlated with stress resistance, indicating that rhizosphere microbes play roles in the regulation of drought-responsive genes (Wang et al., 2005). According to the study of Liu et al. (2020), inoculation of *Arabidopsis* and soybean with *Paenibacillus polymyxa* CR1 induced the expression of the drought-responsive genes *Response to Desiccation 29A* (*RD29A*) and *Response to Desiccation 29B* (*RD29B*) and improved drought resistance. In addition, increases in *RD29A* and *RD29B* mRNA levels were further enhanced when plants encountered *P. polymyxa* CR1 for a second time, indicating that *RD29A* and *RD29B* are “memory genes” for *P. polymyxa* CR1 inoculation. Inoculation of wheat with *Arthrobacter protophormiae* (SA3), *Dietzia natronolimnaea* (STR1), and *B. subtilis* (LDR2) induced the expression of *CONSTITUTIVE TRIPLE RESPONSE 1* (*TaCTR1*), involved in the ethylene signaling pathway, and *DEHYDRATION RESPONSIVE ELEMENT BINDING 2* (*TaDREB2*), a transcription factor gene, thus enhancing plant drought resistance (Barnawal et al., 2017). These studies indicate that regulation of stress-responsive gene expression is a key strategy by which rhizosphere microbes control the drought resistance of host plants.

PGPRs improve osmotic adjustment and antioxidant systems of host crops under drought stress

Osmotic adjustment and the antioxidant defense system are two crucial ways in which plants resist drought stress (Ludlow et al., 1989). According to a series of studies, we found that improvements in the osmotic regulation system and the antioxidant system of host plants were the main ways by which rhizosphere microbes improved plant drought resistance. For example, inoculation of wheat with PGPRs promoted the accumulation of proline and soluble proteins, thus improving drought resistance (Azmat et al., 2020). Inoculation of soybean with the endophytic bacteria *Sphingomonas* sp. promoted the accumulation of compatible sugar solutes and amino acids to improve drought resistance (Asaf et al., 2017). Drought stress is often accompanied by the production of ROS, which can cause oxidative damage to plants (Mittler, 2002). Rhizosphere microbes have been reported to reduce ROS accumulation caused by drought. For example, one study (Batool et al., 2020) found that the PGPR *B. subtilis* HAS31 maintained potato growth and yield under drought stress by activating CAT, POD, SOD, and other antioxidant enzymes. Inoculation of tomato and maize with the ACC deaminase-producing bacteria *B. subtilis* rhizo SF48 or *Pseudomonas fluorescens* strains improved antioxidant enzyme activities, alleviated oxidative damage caused by drought, and improved crop yield (Gowtham et al., 2020; Zarei et al., 2020).

SUMMARY AND PROSPECTS

Improving drought resistance in crop plants is a challenge for plant breeders and crop physiologists, as it is a complex genetic trait that involves multiple pathways. As discussed above, exogenous applications of PGRs and microorganisms are effective strategies for improving plant drought resistance by controlling plant physiological and biochemical characteristics, but the genetic and molecular mechanisms remain largely unclear. Whether exogenous application of these PGRs or microbes will be equally effective in the field is still unknown and requires further study.

Genetic improvement and some exogenous treatments (such as exogenous PGR treatment and microbial inoculation) have been shown to improve crop drought resistance under extreme drought stress. Nonetheless, this does not mean that better yields will ultimately be obtained. Stress resistance and high yield may be mutually exclusive outcomes, as both are energy-consuming processes, and the trade-offs between them are poorly understood. It is possible for us to spray all our fields with ABA: the plants will grow slowly, close their stomata, and probably survive a short-term drought. But in the meantime, stomatal closure will reduce the amount of carbon dioxide absorbed by the leaves, which may lead to a decrease in photosynthetic efficiency. Lack of energy may eventually limit crop yields. In addition, drought is often accompanied by elevated temperatures. Stomatal closure will cause a decrease in transpiration, which is not conducive to a reduction in leaf temperature. To increase both stress tolerance and yield, scientists must make more efforts to balance these potentially competing processes. Using specific drought-inducible promoters to control the expression of functional genes may be a good approach because this strategy reduces energy consumption and ensures the growth of

plants under non-stress conditions (Liu et al., 2019; Chen et al., 2020).

As mentioned above, microorganisms regulate plant drought resistance by regulating plant physiological and biochemical characteristics. Owing to the limitations of traditional technology, the gene network by which root microorganisms regulate host plant drought resistance remains unclear. There are many microbes in natural soil, but a large fraction of them cannot be cultivated in the laboratory, limiting the extent to which we can understand them. The vast majority of previous research on interactions between crops and single microorganisms has been conducted in the laboratory, rarely under natural conditions. Future studies should aim to explore the interactions between the microbiome and host plants, particularly under field conditions.

“Drought” has a wide range of meanings, mostly because of the scales (temporal and spatial) of the events being considered. The temporal and spatial scales at which farmers operate should be the guiding focus. All research aiming to improve drought resistance and reduce yield loss in the field must ultimately be evaluated on farms (Passioura, 2007, 2010). As shown in this review, as plant physiologists or molecular biologists, we have studied and been interested in the performance of plants under sudden and severe drought stress with durations of a few hours or days, and we have evaluated plant drought resistance using some physiological characteristics or survival rates. However, in agricultural production, this type of sudden and severe drought stress is a rare event. The environment is more complex and diverse, and drought is often accompanied by other stresses. Therefore, the key to scaling up drought resistance strategies is to facilitate dialogue among farmers, agronomists, breeders, plant physiologists, and molecular biologists and to connect their work.

FUNDING

This work was supported by grants from the Wuhan Applied Foundational Frontier Project (2020020601012258), the National Natural Science Foundation of China (32061143031), and the Fundamental Research Funds for the Central Universities (2662020SKY009).

AUTHOR CONTRIBUTIONS

H.Z., X.S., and M.D. discussed and wrote the manuscript.

ACKNOWLEDGMENTS

We apologize to the many authors whose work could not be cited owing to space limitations of the review. No conflict of interest declared.

Received: February 13, 2021

Revised: June 20, 2021

Accepted: August 2, 2021

Published: August 4, 2021

REFERENCES

- Abd El-Gawad, H.G., Mukherjee, S., Farag, R., Abd Elbar, O.H., Hikal, M., Abou El-Yazied, A., Abd Elhady, S.A., Helal, N., ElKelish, A., El Nahhas, N., et al. (2021). Exogenous γ -aminobutyric acid (GABA)-induced signaling events and field performance associated with mitigation of drought stress in *Phaseolus vulgaris* L. *Plant Signal. Behav.* 16:1853384.
- Abid, G., Ouertani, R.N., Jebara, S.H., Boubakri, H., Muhovski, Y., Ghouili, E., Abdelkarim, S., Chaieb, O., Hidri, Y., Kadri, S., et al. (2020). Alleviation of drought stress in faba bean (*Vicia faba* L.) by

- exogenous application of β -aminobutyric acid (BABA). *Physiol. Mol. Biol. plants Int. J. Funct. Plant Biol.* **26**:1173–1186.
- Ahmad, S., Kamran, M., Ding, R., Meng, X., Wang, H., Ahmad, I., Fahad, S., and Han, Q. (2019). Exogenous melatonin confers drought stress by promoting plant growth, photosynthetic capacity and antioxidant defense system of maize seedlings. *PeerJ* **7**:e7793.
- Alami, Y., Achouak, W., Marol, C., and Heulin, T. (2000). Rhizosphere soil aggregation and plant growth promotion of sunflowers by an exopolysaccharide-producing *Rhizobium* sp. strain isolated from sunflower roots. *Appl. Environ. Microbiol.* **66**:3393–3398.
- Alcázar, R., Bueno, M., and Tiburcio, A.F. (2020). Polyamines: small amines with large effects on plant abiotic stress tolerance. *Cells* **9**:2373.
- Ali, Q., and Ashraf, M. (2011). Induction of drought tolerance in maize (*Zea mays* L.) due to exogenous application of trehalose: growth, photosynthesis, water relations and oxidative defence mechanism. *J. Agron. Crop Sci.* **197**:258–271.
- Ali, Q., Ashraf, M., and Athar, H.U.R. (2007). Exogenously applied proline at different growth stages enhances growth of two maize cultivars grown under water deficit conditions. *Pakistan J. Bot.* **39**:1133–1144.
- Ali, Q., Anwar, F., Ashraf, M., Saari, N., and Perveen, R. (2013). Ameliorating effects of exogenously applied proline on seed composition, seed oil quality and oil antioxidant activity of maize (*Zea mays* L.) under drought stress. *Int. J. Mol. Sci.* **14**:818–835.
- Armada, E., Roldán, A., and Azcon, R. (2014). Differential activity of autochthonous bacteria in controlling drought stress in native *Lavandula* and *Salvia* plants species under drought conditions in natural arid soil. *Microb. Ecol.* **67**:410–420.
- Arvin, P., Vafabakhsh, J., Mazaheri, D., Noormohamadi, G., and Azizi, M. (2012). Study of drought stress and plant growth promoting rhizobacteria (PGPR) on yield, yield components and seed oil content of different cultivars and species of *brassica oilseed* rape. *Ann. Biol. Res.* **3**:4444–4451.
- Arzanesh, M.H., Alikhani, H.A., Khavazi, K., Rahimian, H.A., and Miransari, M. (2011). Wheat (*Triticum aestivum* L.) growth enhancement by *Azospirillum* sp. under drought stress. *World J. Microbiol. Biotechnol.* **27**:197–205.
- Asaf, S., Khan, A.L., Khan, M.A., Imran, Q.M., Yun, B.W., and Lee, I.J. (2017). Osmoprotective functions conferred to soybean plants via inoculation with *Sphingomonas* sp. LK11 and exogenous trehalose. *Microbiol. Res.* **205**:135–145.
- Awan, S.A., Khan, I., Rizwan, M., Zhang, X., Brestic, M., Khan, A., El-Sheikh, M.A., Alyemeni, M.N., Ali, S., and Huang, L. (2020). Exogenous abscisic acid and jasmonic acid restrain polyethylene glycol-induced drought by improving the growth and antioxidative enzyme activities in pearl millet. *Physiol. Plant.* <https://doi.org/10.1111/ppl.13247>.
- Azmat, A., Yasmin, H., Hassan, M.N., Nosheen, A., Naz, R., Sajjad, M., Ilyas, N., and Akhtar, M.N. (2020). Co-application of bio-fertilizer and salicylic acid improves growth, photosynthetic pigments and stress tolerance in wheat under drought stress. *PeerJ* **8**:e9960.
- Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., and Vivanco, J.M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* **57**:233–266.
- Barnawal, D., Bharti, N., Pandey, S.S., Pandey, A., Chanotiya, C.S., and Kalra, A. (2017). Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and *TaCTR1/TaDREB2* expression. *Physiol. Plant.* **161**:502–514.
- Batool, T., Ali, S., Seleiman, M.F., Naveed, N.H., Ali, A., Ahmed, K., Abid, M., Rizwan, M., Shahid, M.R., Alotaibi, M., et al. (2020). Plant growth promoting rhizobacteria alleviates drought stress in potato in response to suppressive oxidative stress and antioxidant enzymes activities. *Sci. Rep.* **10**:16975.
- Berg, G., and Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol. Ecol.* **68**:1–13.
- Bocchini, M., D'Amato, R., Ciancaleoni, S., Fontanella, M.C., Palmerini, C.A., Beone, G.M., Onofri, A., Negri, V., Marconi, G., Albertini, E., et al. (2018). Soil selenium (Se) biofortification changes the physiological, biochemical and epigenetic responses to water stress in *Zea mays* L. By inducing a higher drought tolerance. *Front. Plant Sci.* **9**:389.
- Cao, M., Liu, X., Zhang, Y., Xue, X., Zhou, X.E., Melcher, K., Gao, P., Wang, F., Zeng, L., Zhao, Y., et al. (2013). An ABA-mimicking ligand that reduces water loss and promotes drought resistance in plants. *Cell Res.* **23**:1043–1054.
- Cao, M.J., Zhang, Y.L., Liu, X., Huang, H., Zhou, X.E., Wang, W.L., Zeng, A., Zhao, C.Z., Si, T., Du, J., et al. (2017). Combining chemical and genetic approaches to increase drought resistance in plants. *Nat. Commun.* **8**:1183.
- Cappellari, L.D.R., Chiappero, J., Santoro, M.V., Giordano, W., and Banchio, E. (2017). Inducing phenolic production and volatile organic compounds emission by inoculating *Mentha piperita* with plant growth-promoting rhizobacteria. *Sci. Horticult.* **220**:193–198.
- Castiglioni, P., Warner, D., Bensen, R.J., Anstrom, D.C., Harrison, J., Stoecker, M., Abad, M., Kumar, G., Salvador, S., D'Ordine, R., et al. (2008). Bacterial RNA chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions. *Plant Physiol.* **147**:446–455.
- Chen, W., Yao, X., Cai, K., and Chen, J. (2011). Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. *Biol. Trace Elem. Res.* **142**:67–76.
- Chen, C., Xin, K., Liu, H., Cheng, J., Shen, X., Wang, Y., and Zhang, L. (2017). *Pantoea alhagi*, a novel endophytic bacterium with ability to improve growth and drought tolerance in wheat. *Sci. Rep.* **7**:41564.
- Chen, J.H., Chen, S.T., He, N.Y., Wang, Q.L., Zhao, Y., Gao, W., and Guo, F.Q. (2020). Nuclear-encoded synthesis of the D1 subunit of photosystem II increases photosynthetic efficiency and crop yield. *Nat. Plants* **6**:570–580.
- Cohen, A.C., Travaglia, C.N., Bottini, R., and Piccoli, P.N. (2009). Participation of abscisic acid and gibberellins produced by endophytic *Azospirillum* in the alleviation of drought effects in maize. *Botany-Botan.* **87**:455–462.
- Danish, S., Zafar-Ul-Hye, M., Mohsin, F., and Hussain, M. (2020). ACC-deaminase producing plant growth promoting rhizobacteria and biochar mitigate adverse effects of drought stress on maize growth. *PLoS One* **15**:e0230615.
- Debnath, B., Islam, W., Li, M., Sun, Y., Lu, X., Mitra, S., Hussain, M., Liu, S., and Qiu, D. (2019). Melatonin mediates enhancement of stress tolerance in plants. *Int. J. Mol. Sci.* **20**:1040.
- Deshpande, S., Manoharan, R., and Mitra, S. (2020). Exogenous β -cyclocitral treatment primes tomato plants against drought by inducing tolerance traits, independent of abscisic acid. *Plant Biol.* <https://doi.org/10.1111/plb.13210>.
- Ding, F., Wang, G., Wang, M., and Zhang, S. (2018). Exogenous melatonin improves tolerance to water deficit by promoting citicute formation in tomato plants. *Molecules (Basel, Switzerland)* **23**:1605.
- Doneva, D., Pál, M., Brankova, L., Szalai, G., Tajti, J., Khalil, R., Ivanovska, B., Velikova, V., Misheva, S., Janda, T., et al. (2021). The effects of putrescine pre-treatment on osmotic stress responses in drought-tolerant and drought-sensitive wheat seedlings. *Physiol. Plant.* **171**:200–216.

- Ebeed, H.T., Hassan, N.M., and Aljarani, A.M. (2017). Exogenous applications of polyamines modulate drought responses in wheat through osmolytes accumulation, increasing free polyamine levels and regulation of polyamine biosynthetic genes. *Plant Physiol. Biochem.* **118**:438–448.
- Elkeilsh, A., Awad, Y.M., Soliman, M.H., Abu-Elsaoud, A., Abdelhamid, M.T., and El-Metwally, I.M. (2019). Exogenous application of β -sitosterol mediated growth and yield improvement in water-stressed wheat (*Triticum aestivum*) involves up-regulated antioxidant system. *J. Plant Res.* **132**:881–901.
- Fan, W., Li, J., Jia, J., Wang, F., Cao, C., Hu, J., and Mu, Z. (2015). Pyrabactin regulates root hydraulic properties in maize seedlings by affecting PIP aquaporins in a phosphorylation-dependent manner. *Plant Physiol. Biochem.* **94**:28–34.
- Farooq, M., Wahid, A., and Lee, D.J. (2009). Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. *Acta Physiolog. Plant.* **31**:937–945.
- Gevrek, M.N., and Atasoy, G.D. (2012). Effect of post anthesis drought on certain agronomical characteristics of wheat under two different nitrogen application conditions. *Turkish J. Field Crops* **17**:19–23.
- Ghafoor, R., Akram, N.A., Rashid, M., Ashraf, M., Iqbal, M., and Lixin, Z. (2019). Exogenously applied proline induced changes in key anatomical features and physio-biochemical attributes in water stressed oat (*Avena sativa* L.) plants. *Physiol. Mol. Biol. Plants* **25**:1121–1135.
- Gou, W., Zheng, P., Tian, L., Gao, M., Zhang, L., Akram, N.A., and Ashraf, M. (2017). Exogenous application of urea and a urease inhibitor improves drought stress tolerance in maize (*Zea mays* L.). *J. Plant Res.* **130**:599–609.
- Gowtham, H.G., Brijesh Singh, S., Murali, M., Shilpa, N., Prasada, M., Aiyaza, M., Amruthesh, K.N., and Niranjana, S.R. (2020). Induction of drought tolerance in tomato upon the application of ACC deaminase producing plant growth promoting rhizobacterium *Bacillus subtilis* Rhizo SF48. *Microbiol. Res.* **234**:126422.
- Guo, J.H., Liu, X.J., Zhang, Y., Shen, J.L., Han, W.X., Zhang, W.F., Christie, P., Goulding, K.W., Vitousek, P.M., and Zhang, F.S. (2010). Significant acidification in major Chinese croplands. *Science* **327**:1008–1010.
- Gupta, S., Agarwal, V.P., and Gupta, N.K. (2012). Efficacy of putrescine and benzyladenine on photosynthesis and productivity in relation to drought tolerance in wheat (*Triticum aestivum* L.). *Physiol. Mol. Biol. Plants* **18**:331–336.
- Gupta, A., Rico-Medina, A., and Caño-Delgado, A.I. (2020a). The physiology of plant responses to drought. *Science* **368**:266–269.
- Gupta, M.K., Lenka, S.K., Gupta, S., and Rawal, R.K. (2020b). Agonist, antagonist and signaling modulators of ABA receptor for agronomic and post-harvest management. *Plant Physiol. Biochem.* **148**:10–25.
- Habibi, G. (2012). Exogenous salicylic acid alleviates oxidative damage of barley plants under drought stress. *Acta Biologica Szegediensis* **56**:57–63.
- Hardeland, R. (2015). Melatonin in plants and other phototrophs: advances and gaps concerning the diversity of functions. *J. Exp. Bot.* **66**:627–646.
- Hasanuzzaman, M., Nahar, K., Rahman, A., Inafuku, M., Oku, H., and Fujita, M. (2018). Exogenous nitric oxide donor and arginine provide protection against short-term drought stress in wheat seedlings. *Physiol. Mol. Biol. Plants* **24**:993–1004.
- Hashem, A., Tabassum, B., and Fathi Abd Allah, E. (2019). *Bacillus subtilis*: a plant-growth promoting *Rhizobacterium* that also impacts biotic stress. *Saudi J. Biol. Sci.* **26**:1291–1297.
- Hassan, N., Ebeed, H., and Aljaarany, A. (2020). Exogenous application of spermine and putrescine mitigate adversities of drought stress in wheat by protecting membranes and chloroplast ultra-structure. *Physiol. Mol. Biol. Plants* **26**:233–245.
- He, Z., Zhong, J., Sun, X., Wang, B., Terzaghi, W., and Dai, M. (2018). The maize ABA receptors ZmPYL8, 9, and 12 facilitate plant drought resistance. *Front. Plant Sci.* **9**:422.
- He, Z., Wu, J., Sun, X., and Dai, M. (2019). The maize clade A PP2C phosphatases play critical roles in multiple abiotic stress responses. *Int. J. Mol. Sci.* **20**:3573.
- Holopainen, J.K., and Gershenzon, J. (2010). Multiple stress factors and the emission of plant VOCs. *Trends Plant Sci.* **15**:176–184.
- Hu, W., Cao, Y., Loka, D.A., Harris-Shultz, K.R., Reiter, R.J., Ali, S., Liu, Y., and Zhou, Z. (2020). Exogenous melatonin improves cotton (*Gossypium hirsutum* L.) pollen fertility under drought by regulating carbohydrate metabolism in male tissues. *Plant Physiol. Biochem.* **151**:579–588.
- Huan, L., Jin-Qiang, W., and Qing, L. (2020). Photosynthesis product allocation and yield in sweet potato with spraying exogenous hormones under drought stress. *J. Plant Physiol.* **253**:153265.
- Huang, B., Chen, Y.E., Zhao, Y.Q., Ding, C.B., Liao, J.Q., Hu, C., Zhou, L.J., Zhang, Z.W., Yuan, S., and Yuan, M. (2019). Exogenous melatonin alleviates oxidative damages and protects photosystem II in maize seedlings under drought stress. *Front. Plant Sci.* **10**:677.
- Hussain, I., Rasheed, R., Ashraf, M.A., Mohsin, M., Shah, S., Rashid, D.A., Akram, M., Nisar, J., and Riaz, M. (2020). Foliar applied acetylsalicylic acid induced growth and key-biochemical changes in chickpea (*Cicer arietinum* L.) under drought stress. *Dose-Response* **18**, 1559325820956801.
- Hussein, H.A., Mekki, B.B., El-Sadek, M., and El Lateef, E.E. (2019). Effect of L-ornithine application on improving drought tolerance in sugar beet plants. *Heliyon* **5**:e02631.
- Igarashi, K., and Kashiwagi, K. (2019). The functional role of polyamines in eukaryotic cells. *Int. J. Biochem. Cell Biol.* **107**:104–115.
- Iqbal, M.S., Jabbar, B., Sharif, M.N., Ali, Q., Husnain, T., and Nasir, I.A. (2017). In silico MCMV silencing concludes potential host-derived miRNAs in maize. *Front. Plant Sci.* **8**:372.
- Iturriaga, G., Suárez, R., and Nova-Franco, B. (2009). Trehalose metabolism: from osmoprotection to signaling. *Int. J. Mol. Sci.* **10**:3793–3810.
- Jiao, Z., Li, Y., Li, J., Xu, X., Li, H., Lu, D., and Wang, J. (2012). Effects of exogenous chitosan on physiological characteristics of potato seedlings under drought stress and rehydration. *Potato Res.* **55**:293–301.
- Joshi, R., Sahoo, K.K., Singh, A.K., Anwar, K., Pundir, P., Gautam, R.K., Krishnamurthy, S.L., Sopory, S.K., Pareek, A., and Singla-Pareek, S.L. (2020). Enhancing trehalose biosynthesis improves yield potential in marker-free transgenic rice under drought, saline, and sodic conditions. *J. Exp. Bot.* **71**:653–668.
- Kohler, J., Hernández, J.A., Caravaca, F., and Roldán, A. (2008). Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. *Funct. Plant Biol.* **35**:141–151.
- Kosar, F., Akram, N.A., Ashraf, M., Ahmad, A., Alyemeni, M.N., and Ahmad, P. (2020). Impact of exogenously applied trehalose on leaf biochemistry, achene yield and oil composition of sunflower under drought stress. *Physiol. Plant.* <https://doi.org/10.1111/pp1.13155>.
- Kubiś, J. (2005). The effect of exogenous spermidine on superoxide dismutase activity, H₂O₂ and superoxide radical level in barley leaves under water deficit conditions. *Acta Physiolog. Plant.* **27**:289–295.

- Lakshmanan, V., Ray, P., and Craven, K.D. (2017). Toward a resilient, functional microbiome: drought tolerance-alleviating microbes for sustainable agriculture. *Methods Mol. Biol.* **1631**:69–84.
- Latif, M., Akram, N.A., and Ashraf, M. (2016). Regulation of some biochemical attributes in drought-stressed cauliflower (*Brassica oleracea* L.) by seed pre-treatment with ascorbic acid. *J. Hortic. Sci. Biotechnol.* **91**:129–137.
- Li, L., Gu, W., Li, J., Li, C., Xie, T., Qu, D., Meng, Y., Li, C., and Wei, S. (2018a). Exogenously applied spermidine alleviates photosynthetic inhibition under drought stress in maize (*Zea mays* L.) seedlings associated with changes in endogenous polyamines and phytohormones. *Plant Physiol. Biochem.* **129**:35–55.
- Liu, S., Wang, X., Wang, H., Xin, H., Yang, X., Yan, J., Li, J., Tran, L.S., Shinozaki, K., Yamaguchi-Shinozaki, K., et al. (2013a). Genome-wide analysis of *ZmDREB* genes and their association with natural variation in drought tolerance at seedling stage of *Zea mays* L. *PLoS Genet.* **9**:e1003790.
- Liu, X.J., Zhang, Y., Han, W.X., Tang, A.H., Shen, J.L., Cui, Z.L., Vitousek, P., Erisman, J.W., Goulding, K., Christie, P., et al. (2013b). Enhanced nitrogen deposition over China. *Nature* **494**:459–462.
- Liu, J., Wang, W., Wang, L., and Sun, Y. (2015). Exogenous melatonin improves seedling health index and drought tolerance in tomato. *Plant Growth Regul.* **77**:317–326.
- Liu, Y., Liang, H., Lv, X., Liu, D., Wen, X., and Liao, Y. (2016). Effect of polyamines on the grain filling of wheat under drought stress. *Plant Physiol. Biochem.* **100**:113–129.
- Liu, C.Y., Zhang, F., Zhang, D.J., Srivastava, A.K., Wu, Q.S., and Zou, Y.N. (2018). Mycorrhiza stimulates root-hair growth and IAA synthesis and transport in trifoliate orange under drought stress. *Sci. Rep.* **8**:1978.
- Liu, M., Shi, Z., Zhang, X., Wang, M., Zhang, L., Zheng, K., Liu, J., Hu, X., Di, C., Qian, Q., et al. (2019). Inducible overexpression of Ideal Plant Architecture1 improves both yield and disease resistance in rice. *Nat. plants* **5**:389–400.
- Liu, W., Sikora, E., and Park, S.W. (2020). Plant growth-promoting rhizobacterium, *Paenibacillus polymyxa* CR1, upregulates dehydration-responsive genes, *RD29A* and *RD29B*, during priming drought tolerance in *Arabidopsis*. *Plant Physiol. Biochem.* **156**:146–154.
- Liu, T., Li, C.X., Zhong, J., Shu, D., Luo, D., Li, Z.M., Zhou, J.Y., Yang, J., Tan, H., and Ma, X.R. (2021). Exogenous 1',4'-trans-diol-ABA induces stress tolerance by affecting the level of gene expression in tobacco (*Nicotiana tabacum* L.). *Int. J. Mol. Sci.* **22**:2555.
- Ludlow, M.M. (1989). Strategies of Response to Water Stress. Structural and Functional Responses to Environmental Stresses. In The Hague, K. H. Kreeb., H. Richter., and T. M. Hinckley., eds. (SPB Academic), pp. 269–281.
- Lunn, J.E., Delorge, I., Figueroa, C.M., Van Dijck, P., and Stitt, M. (2014). Trehalose metabolism in plants. *Plant J.* **79**:544–567.
- Mao, H., Wang, H., Liu, S., Li, Z., Yang, X., Yan, J., Li, J., Tran, L.S., and Qin, F. (2015). A transposable element in a NAC gene is associated with drought tolerance in maize seedlings. *Nat. Commun.* **6**:8326.
- Marcinińska, I., Dziurka, K., Waligórski, P., Janowiak, F., Skrzypek, E., Warchol, M., Juzoń, K., Kapłoniak, K., and Czyczyło-Mysza, I.M. (2020). Exogenous polyamines only indirectly induce stress tolerance in wheat growing in hydroponic culture under polyethylene glycol-induced osmotic stress. *Life (Basel, Switzerland)* **10**:151.
- Mayak, S., Tirosch, T., and Glick, B.R. (2004). Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. *Plant Sci.* **166**:525–530.
- Mendes, R., Garbeva, P., and Raaijmakers, J.M. (2013). The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol. Rev.* **37**:634–663.
- Mirajkar, S.J., Dalvi, S.G., Ramteke, S.D., and Suprasanna, P. (2019). Foliar application of gamma radiation processed chitosan triggered distinctive biological responses in sugarcane under water deficit stress conditions. *Int. J. Biol. Macromolecules* **139**:1212–1223.
- Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* **7**:405–410.
- Moschou, P.N., and Roubelakis-Angelakis, K.A. (2014). Polyamines and programmed cell death. *J. Exp. Bot.* **65**:1285–1296.
- Nadeem, S.M., Ahmad, M., Tufail, M.A., Asghar, H.N., Nazli, F., and Zahir, Z.A. (2020). Appraising the potential of EPS-producing rhizobacteria with ACC-deaminase activity to improve growth and physiology of maize under drought stress. *Physiol. Plant.* <https://doi.org/10.1111/ppl.13212>.
- Naseem, H., Ahsan, M., Shahid, M.A., and Khan, N. (2018). Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. *J. Basic Microbiol.* **58**:1009–1022.
- Naveed, M., Mitter, B., Reichenauer, T.G., Wiecek, K., and Sessitsch, A. (2014). Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* psjn and *Enterobacter* sp. fd17. *Environ. Exp. Bot.* **97**:30–39.
- Nawaz, F., Ashraf, M.Y., Ahmad, R., and Waraich, E.A. (2013). Selenium (Se) seed priming induced growth and biochemical changes in wheat under water deficit conditions. *Biol. Trace Elem. Res.* **151**:284–293.
- Nawaz, F., Ashraf, M.Y., Ahmad, R., Waraich, E.A., and Shabbir, R.N. (2014). Selenium (Se) regulates seedling growth in wheat under drought stress 2014:670–675.
- Nawaz, F., Ashraf, M.Y., Ahmad, R., Waraich, E.A., Shabbir, R.N., and Bukhari, M.A. (2015). Supplemental selenium improves wheat grain yield and quality through alterations in biochemical processes under normal and water deficit conditions. *Food Chem.* **175**:350–357.
- Okamoto, M., Peterson, F.C., Defries, A., Park, S.Y., Endo, A., Nambara, E., Volkman, B.F., and Cutler, S.R. (2013). Activation of dimeric ABA receptors elicits guard cell closure, ABA-regulated gene expression, and drought tolerance. *Proc. Natl. Acad. Sci. U S A* **110**:12132–12137.
- Park, S.Y., Fung, P., Nishimura, N., Jensen, D.R., Fujii, H., Zhao, Y., Lumba, S., Santiago, J., Rodrigues, A., Chow, T.F., et al. (2009). Abscissic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science* **324**:1068–1071.
- Passioura, J. (2007). The drought environment: physical, biological and agricultural perspectives. *J. Exp. Bot.* **58**:113–117.
- Passioura, J. (2010). Scaling up: the essence of effective agricultural research. *Funct. Plant Biol.* **37**:585–591.
- Puli, M.R., and Raghavendra, A.S. (2012). Pyrabactin, an ABA agonist, induced stomatal closure and changes in signalling components of guard cells in abaxial epidermis of *Pisum sativum*. *J. Exp. Bot.* **63**:1349–1356.
- Qiao, Y., Ren, J., Yin, L., Liu, Y., Deng, X., Liu, P., and Wang, S. (2020). Exogenous melatonin alleviates PEG-induced short-term water deficiency in maize by increasing hydraulic conductance. *BMC Plant Biol.* **20**:218.
- Rasheed, R., Yasmeen, H., Hussain, I., Iqbal, M., Ashraf, M.A., and Parveen, A. (2020). Exogenously applied 5-aminolevulinic acid modulates growth, secondary metabolism and oxidative defense in sunflower under water deficit stress. *Physiol. Mol. Biol. Plants* **26**:489–499.
- Raza, M.A.S., Saleem, M.F., Anjum, S.A., Khaliq, T., and Wahid, M.A. (2012). Foliar application of potassium under water deficit conditions

- improved the growth and yield of wheat (*Triticum aestivum* L.). *J. Anim. Plant Sci.* **22**:431–437.
- Roberson, E.B., and Firestone, M.K. (1992). Relationship between desiccation and exopolysaccharide production in a soil *Pseudomonas* sp. *Appl. Environ. Microbiol.* **58**:1284–1291.
- Roessner, U., Luedemann, A., Brust, D., Fiehn, O., Linke, T., Willmitzer, L., and Fernie, A. (2001). Metabolic profiling allows comprehensive phenotyping of genetically or environmentally modified plant systems. *Plant Cell* **13**:11–29.
- Rojas-Solís, D., Zetter-Salmón, E., Contreras-Pérez, M., Rocha-Granados, M., del, C., Macías-Rodríguez, L., and Santoyo, G. (2018). *Pseudomonas stutzeri* E25 and *Stenotrophomonas maltophilia* CR71 endophytes produce antifungal volatile organic compounds and exhibit additive plant growth-promoting effects. *Biocatal. Agric. Biotechnol.* **13**:46–52.
- Rout, M.E., and Southworth, D. (2013). The root microbiome influences scales from molecules to ecosystems: the unseen majority. *Am. J. Bot.* **100**:1689–1691.
- Sandhya, V., Ali, S.Z., Grover, M., Reddy, G., and Venkateswarlu, B. (2009). Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *pseudomonas putida* strain gap-p45. *Biol. Fertil. Soils* **46**:17–26.
- Santos-Medellín, C., Edwards, J., Liechty, Z., Nguyen, B., and Sundaresan, V. (2017). Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *mBio* **8**:e00764-17.
- Schulz-Bohm, K., Gerards, S., Hundscheid, M., Melenhorst, J., de Boer, W., and Garbeva, P. (2018). Calling from distance: attraction of soil bacteria by plant root volatiles. *ISME J.* **12**:1252–1262.
- Sezgin, A., Altuntas, C., Demiralay, M., Cinemre, S., and Terzi, R. (2019). Exogenous alpha lipoic acid can stimulate photosystem II activity and the gene expressions of carbon fixation and chlorophyll metabolism enzymes in maize seedlings under drought. *J. Plant Physiol.* **232**:65–73.
- Shabbir, R.N., Ashraf, M.Y., Waraich, E.A., Ahmad, R., and Shahbaz, M. (2015). Combined effects of drought stress and npk foliar spray on growth, physiological processes and nutrient uptake in wheat. *Pakistan J. Bot.* **47**:1207–1216.
- Shabbir, R.N., Waraich, E.A., Ali, H., Nawaz, F., Ashraf, M.Y., Ahmad, R., Awan, M.I., Ahmad, S., Irfan, M., Hussain, S., et al. (2016). Supplemental exogenous NPK application alters biochemical processes to improve yield and drought tolerance in wheat (*Triticum aestivum* L.). *Environ. Sci. Pollut. Res. Int.* **23**:2651–2662.
- Sharma, M., Gupta, S.K., Majumder, B., Maurya, V.K., Deeba, F., Alam, A., and Pandey, V. (2017). Salicylic acid mediated growth, physiological and proteomic responses in two wheat varieties under drought stress. *J. Proteomics* **163**:28–51.
- Shaw, A.K., Bhardwaj, P.K., Ghosh, S., Roy, S., Saha, S., Sherpa, A.R., Saha, S.K., and Hossain, Z. (2016). β -Aminobutyric acid mediated drought stress alleviation in maize (*Zea mays* L.). *Environ. Sci. Pollut. Res. Int.* **23**:2437–2453.
- Shehzad, M.A., Nawaz, F., Ahmad, F., Ahmad, N., and Masood, S. (2020). Protective effect of potassium and chitosan supply on growth, physiological processes and antioxidative machinery in sunflower (*Helianthus annuus* L.) under drought stress. *Ecotoxicology Environ. Saf.* **187**:109841.
- Shemi, R., Wang, R., Gheith, E., Hussain, H.A., Hussain, S., Irfan, M., Cholidah, L., Zhang, K., Zhang, S., and Wang, L. (2021). Effects of salicylic acid, zinc and glycine betaine on morpho-physiological growth and yield of maize under drought stress. *Scientific Rep.* **11**:3195.
- Silveira, N.M., Frungillo, L., Marcos, F.C., Pelegrino, M.T., Miranda, M.T., Seabra, A.B., Salgado, I., Machado, E.C., and Ribeiro, R.V. (2016). Exogenous nitric oxide improves sugarcane growth and photosynthesis under water deficit. *Planta* **244**:181–190.
- Sofy, M.R. (2015). Application of salicylic acid and zinc improves wheat yield through physiological processes under different levels of irrigation intervals. *Int. J. Plant Res.* **5**:136–156.
- Spence, C., Alff, E., Johnson, C., Ramos, C., Donofrio, N., Sundaresan, V., and Bais, H. (2014). Natural rice rhizospheric microbes suppress rice blast infections. *BMC Plant Biol.* **14**:130.
- Tardieu, F. (2012). Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. *J. Exp. Bot.* **63**:25–31.
- Tayyab, N., Naz, R., Yasmin, H., Nosheen, A., Keyani, R., Sajjad, M., Hassan, M.N., and Roberts, T.H. (2020). Combined seed and foliar pre-treatments with exogenous methyl jasmonate and salicylic acid mitigate drought-induced stress in maize. *PLoS One* **15**:e0232269.
- Tian, J., Wang, C., Xia, J., Wu, L., Xu, G., Wu, W., Li, D., Qin, W., Han, X., Chen, Q., et al. (2018). Potential applications of polyamines in agriculture and plant biotechnology. *Methods Mol. Biol. (Clifton, N.J.)* **1694**:489–508.
- Tisarum, R., Theerawitaya, C., Samphumphuang, T., Singh, H.P., and Cha-Um, S. (2020). Foliar application of glycine betaine regulates soluble sugars and modulates physiological adaptations in sweet potato (*Ipomoea batatas*) under water deficit. *Protoplasma* **257**:197–211.
- Vaidya, A.S., Helander, J., Peterson, F.C., Elzinga, D., Dejonghe, W., Kaundal, A., Park, S.Y., Xing, Z., Mega, R., Takeuchi, J., et al. (2019). Dynamic control of plant water use using designed ABA receptor agonists. *Science* **366**:eaaw8848.
- Verma, A.K. (2016). Abiotic stress and crop improvement: current scenario. *Adv. Plants Agric. Res.* **4**. <https://doi.org/10.15406/apar.2016.04.00149>.
- Veroneze-Júnior, V., Martins, M., McLeod, L., Souza, K., Santos-Filho, P.R., Magalhães, P.C., Carvalho, D.T., Santos, M.H., and Souza, T.C. (2020). Leaf application of chitosan and physiological evaluation of maize hybrids contrasting for drought tolerance under water restriction. *Braz. J. Biol.* **80**:631–640.
- Volpe, V., Chitarra, W., Cascone, P., Volpe, M.G., Bartolini, P., Moneti, G., Pieraccini, G., Di Serio, C., Maserti, B., Guerrieri, E., et al. (2018). The association with two different arbuscular mycorrhizal fungi differently affects water stress tolerance in tomato. *Front. Plant Sci.* **9**:1480.
- de Vries, F.T., Griffiths, R.I., Knight, C.G., Nicolitch, O., and Williams, A. (2020). Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science (New York, N.Y.)* **368**:270–274.
- Vurukonda, S.S., Vardharajula, S., Shrivastava, M., and SkZ, A. (2016). Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol. Res.* **184**:13–24.
- Walters, W.A., Jin, Z., Youngblut, N., Wallace, J.G., Sutter, J., Zhang, W., González-Peña, A., Peiffer, J., Koren, O., Shi, Q., et al. (2018). Large-scale replicated field study of maize rhizosphere identifies heritable microbes. *Proc. Natl. Acad. Sci. United States America* **115**:7368–7373.
- Wang, Y., Ohara, Y., Nakayashiki, H., Tosa, Y., and Mayama, S. (2005). Microarray analysis of the gene expression profile induced by the endophytic plant growth-promoting rhizobacteria, *Pseudomonas fluorescens* FPT9601-T5 in *Arabidopsis*. *Mol. Plant-Microbe Interactions: MPMI* **18**:385–396.
- Wang, X., Wang, H., Liu, S., Ferjani, A., Li, J., Yan, J., Yang, X., and Qin, F. (2016). Genetic variation in *ZmVPP1* contributes to drought tolerance in maize seedlings. *Nat. Genet.* **48**:1233–1241.

- Wang, G., Xiao, Y., Deng, X., Zhang, H., Li, T., and Chen, H. (2018). Exogenous hydrogen peroxide contributes to heme oxygenase-1 delaying programmed cell death in isolated aleurone layers of rice subjected to drought stress in a cGMP-dependent manner. *Front. Plant Sci.* **9**:84.
- Wei, L., Wang, L., Yang, Y., Wang, P., Guo, T., and Kang, G. (2015). Abscisic acid enhances tolerance of wheat seedlings to drought and regulates transcript levels of genes encoding ascorbate-glutathione biosynthesis. *Front. Plant Sci.* **6**:458.
- Wezel, A., Casagrande, M., Celette, F., Vian, J.F., Ferrer, A., and Peigné, J. (2014). Agroecological practices for sustainable agriculture. a review. *Agron. Sustain. Dev.* **34**:1–20.
- White, P.J., and Brown, P.H. (2010). Plant nutrition for sustainable development and global health. *Ann. Bot.* **105**:1073–1080.
- Xiang, Y., Sun, X., Gao, S., Qin, F., and Dai, M. (2017). Deletion of an endoplasmic reticulum stress response element in a *ZmPP2C-A* gene facilitates drought tolerance of maize seedlings. *Mol. Plant* **10**:456–469.
- Xiao, W., Fu-lai, L., and Dong, J. (2017). Priming: a promising strategy for crop production in response to future climate. *J. Integr. Agric.* **16**:60345–60352.
- Xie, T., Gu, W., Wang, M., Zhang, L., Li, C., Li, C., Li, W., Li, L., and Wei, S. (2019). Exogenous 2-(3,4-dichlorophenoxy) triethylamine ameliorates the soil drought effect on nitrogen metabolism in maize during the pre-female inflorescence emergence stage. *BMC Plant Biol.* **19**:107.
- Xu, L., Islam, F., Ali, B., Pei, Z., Li, J., Ghani, M.A., and Zhou, W. (2017). Silicon and water-deficit stress differentially modulate physiology and ultrastructure in wheat (*Triticum aestivum* L.). *3 Biotech.* **7**:273.
- Xu, L., Naylor, D., Dong, Z., Simmons, T., Pierroz, G., Hixson, K.K., Kim, Y.M., Zink, E.M., Engbrecht, K.M., Wang, Y., et al. (2018). Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *Proc. Natl. Acad. Sci. United States America* **115**:E4284–E4293.
- Yasmin, H., Rashid, U., Hassan, M.N., Nosheen, A., Naz, R., Ilyas, N., Sajjad, M., Azmat, A., and Alyemeni, M.N. (2020). Volatile organic compounds produced by *Pseudomonas pseudoalcaligenes* alleviated drought stress by modulating defense system in maize (*Zea mays* L.). *Physiologia Plantarum* <https://doi.org/10.1111/ppl.13304>.
- Zarei, T., Moradi, A., Kazemeini, S.A., Akhgar, A., and Rahi, A.A. (2020). The role of ACC deaminase producing bacteria in improving sweet corn (*Zea mays* L. var *saccharata*) productivity under limited availability of irrigation water. *Scientific Rep.* **10**:20361.
- Zhang, L., Gao, M., Hu, J., Zhang, X., Wang, K., and Ashraf, M. (2012). Modulation role of abscisic acid (ABA) on growth, water relations and glycinebetaine metabolism in two maize (*Zea mays* L.) cultivars under drought stress. *Int. J. Mol. Sci.* **13**:3189–3202.
- Zhang, J., Liu, Y.X., Zhang, N., Hu, B., Jin, T., Xu, H., Qin, Y., Yan, P., Zhang, X., Guo, X., et al. (2019a). NRT1.1B is associated with root microbiota composition and nitrogen use in field-grown rice. *Nat. Biotechnol.* **37**:676–684.
- Zhang, M., He, S., Zhan, Y., Qin, B., Jin, X., Wang, M., Zhang, Y., Hu, G., Teng, Z., and Wu, Y. (2019b). Exogenous melatonin reduces the inhibitory effect of osmotic stress on photosynthesis in soybean. *PLoS One* **14**:e0226542.
- Zhang, H., Xiang, Y., He, N., Liu, X., Liu, H., Fang, L., Zhang, F., Sun, X., Zhang, D., Li, X., et al. (2020a). Enhanced vitamin C production mediated by an ABA-induced PTP-like nucleotidase improves plant drought tolerance in *Arabidopsis* and maize. *Mol. Plant* **13**:760–776.
- Zhang, X., Mi, Y., Mao, H., Liu, S., Chen, L., and Qin, F. (2020b). Genetic variation in *ZmTIP1* contributes to root hair elongation and drought tolerance in maize. *Plant Biotechnol. J.* **18**:1271–1283.
- Zhang, M., He, S., Qin, B., Jin, X., Wang, M., Ren, C., Cao, L., and Zhang, Y. (2020c). Exogenous melatonin reduces the inhibitory effect of osmotic stress on antioxidant properties and cell ultrastructure at germination stage of soybean. *PLoS One* **15**:e0243537.
- Zhou, X., Chen, Y., Zhao, Y., Gao, F., and Liu, H. (2020). The application of exogenous PopW increases the tolerance of *Solanum lycopersicum* L. to drought stress through multiple mechanisms. *Physiol. Mol. Biol. Plants* **26**:2521–2535.
- Zhu, J.K. (2016). Abiotic stress signaling and responses in plants. *Cell* **167**:313–324.
- Zhu, Y., and Gong, H. (2013). Beneficial effects of silicon on salt and drought tolerance in plants. *Agron. Sustain. Dev.* **34**:455–472.