

Drought Stress Amelioration Attributes of Plant-Associated Microbiome on Agricultural Plants

Victor Funso Agunbiade and Olubukola Oluranti Babalola 

Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa.

Bioinformatics and Biology Insights
Volume 18: 1–12
© The Author(s) 2024
Article reuse guidelines:
sagepub.com/journals-permissions
DOI: 10.1177/11779322241233442



ABSTRACT: The future global food security depends on the availability of water for agriculture. Yet, the ongoing rise in nonagricultural uses for water, such as urban and industrial uses, and growing environmental quality concerns have increased pressure of irrigation water demand and posed danger to food security. Nevertheless, its severity and duration are predicted to rise shortly. Drought pressure causes stunted growth, severe damage to photosynthesis activity, loss in crop yield, reduced seed germination, and reduced nutrient intake by plants. To overcome the effects of a devastating drought on plants, it is essential to think about the causes, mechanisms of action, and long-term agronomy management and genetics. As a result, there is an urgent need for long-term medication to deal with the harmful effects of drought pressure. The review focuses on the adverse impact of drought on the plant, physiological, and biochemical aspects, and management measures to control the severity of drought conditions. This article reviews the role of genome editing (GE) technologies such as CRISPR 9 (CRISPR-Cas9) related spaces and short palindromic relapse between proteins in reducing the effects of phytohormones, osmolytes, external compounds, proteins, microbes (plant growth-promoting microorganism [PGPM]), approach omics, and drought on plants that support plant growth. This research is to examine the potential of using the microbiome associated with plants for drought resistance and sustainable agriculture. Researchers also advocate using a mix of biotechnology, agronomic, and advanced GE technologies to create drought-tolerant plant varieties.

KEYWORDS: Crop improvement, crop yields, climate change, endophytic microbes, food security, sustainable agriculture

RECEIVED: March 26, 2023. **ACCEPTED:** February 1, 2024.

TYPE: Review

FUNDING: The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: OOB recognized the National Research Foundation of South Africa for the grants (UID: 123634; 132595) that support work in her research group.

DECLARATION OF CONFLICTING INTERESTS: The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

CORRESPONDING AUTHOR: Olubukola Oluranti Babalola, Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho 2531, South Africa. Email: olubukola.babalola@nwu.ac.za

Introduction

Population growth, drastic climate change, water supply, availability of workable land, and biodiversity losses have caused major changes to the global food security.^{1,2} Abiotic stress factors such as drought, salinity, floods, heat, cold, heavy metal pollution, toxic compounds, and biotic stress affect plant growth and yield.^{3,4} Drought pressures have become the most critical and critical constraints, and negatively affect agricultural output and ultimately endangering food security.⁵ Drought affects agricultural output while exacerbating neglect, soil depletion, and environmental damage. Consequently, water scarcity has been identified as a significant worldwide ecological problem.⁶ This abiotic stress leads to substantial physiological, metabolic, and molecular changes in plants, thus decreasing agricultural yields.⁷ With current technologies, researchers have made tremendous progress in recent years to unravel the genetic, biochemical, and signaling mechanisms associated with plant stress responses.^{8–10} The complex process that distinguishes resistance and vulnerability within crop species is not well known.¹¹ Drought stress affects a variety of morphological biochemical parameters, including a decrease in the leaf area, a total reduction in chlorophyll content, leaf wilting, lengthening of the roots, and the formation of reactive oxygen species (ROS).^{4,12,13} Under stress, several osmotic pressure decomposes amass in plant cells, such as proline, glycine betaine (GB), soluble sugars, and spermines, to sustain cell penetration ability.¹⁴ Catalase (CAT), superoxide dismutase (SOD), glutathione reductase

(GR), and ascorbate peroxidase (APX) are examples of oxidation-protective enzymes, known to be altered in drought-stressed plants.¹⁵ Drought stress, on the contrary, alters the expression of a large number of genes, including those involved in the transmission of stress signals; hundreds of functional proteins are also transcribed and controlled, which play a crucial role in drought-tolerant gene expression patterns.¹⁶ As a result, to maintain or raise global food production, sustainable agricultural biotechnology must be developed to ameliorate abiotic stress. Various techniques, including genetic engineering and traditional plant breeding methods, have been used worldwide to improve crop drought tolerance.^{17,18}

CRISPR/Cas9 is a gene-editing technology that enables precise changes to DNA in living organisms. It targets specific DNA sequences using RNA and Cas9 protein. This technology can correct genetic mutations, treat diseases, develop new therapies, and understand biological processes. It holds immense potential in medicine, agriculture, and biotechnology. CRISPR/Cas9 is a precise and effective technique that enables researchers to specifically alter an organism's DNA. To make alterations, such as gene deletion, gene insertion, or gene editing, the Cas9 enzyme is guided by a guide RNA molecule to a specific site in the genome.¹⁹

The genes involved in plant-microbe interactions can be altered using GE techniques like CRISPR/Cas9 to lessen the impact of plant growth-promoting microorganism (PGPM) on plants. For instance, by focusing on particular genes that



Creative Commons Non Commercial CC BY-NC: This article is distributed under the terms of the Creative Commons Attribution-NonCommercial 4.0 License (<https://creativecommons.org/licenses/by-nc/4.0/>) which permits non-commercial use, reproduction and distribution of the work without further permission provided the original work is attributed as specified on the SAGE and Open Access pages (<https://us.sagepub.com/en-us/nam/open-access-at-sage>).

recognize and react to particular phytohormones or osmolytes, researchers may be able to change how sensitive or responsive the plant is to these substances.²⁰

Genome editing can also be used to change genes that are involved in the absorption or metabolism of exogenous substances, such as pesticides or herbicides, lessening the effect these substances have on plants. It may be able to improve tolerance or resistance by carefully modifying the genes responsible for the plant's reaction to these chemicals.²¹

In addition, plants with improved resistance to hazardous bacteria or diseases can be created using GE technology. Researchers may be able to improve the plant's capacity to identify and react to microbial invaders by focusing on specific genes involved in plant defense systems, which might lessen the impacts of PGPM.²² It is important to note that the application of GE technologies in agriculture is still an active area of research and development. While these technologies hold immense promise, their use is subject to regulatory frameworks and ethical considerations. Ongoing studies are being conducted to further explore the potential benefits and implications of GE in reducing the effects of PGPM on plants.²³ It is significant to emphasize that research and development on the use of GE technologies in agriculture is currently ongoing.²⁴ Although these technologies have great potential, their usage is constrained by legal and moral standards. Research is ongoing to examine the possible advantages and consequences of GE in minimizing the impacts of PGPM on plants.²⁵ An introductory approach is to use drought-tolerant biological inoculations or plant growth-promoting rhizobacteria (PGPR) as an option for agricultural production in water-scarce areas. Various research suggested by researchers validates the idea that PGPR can help plants tolerate nonbiological stressors by altering their genetic responses.²⁶ Plant growth-promoting rhizobacteria promise to change the physiological response to water shortage and enhance their drought resistance.²⁷ Multidisciplinary solutions are needed to take full advantage of the potential of microorganisms in agricultural production systems. Data-driven poly-omic science improves our knowledge of microbe structure, dynamics, and composition and their physical function in a variety of designs and ecosystems, like root-to-root, where microbial interactions at the community level guide plant reactions to multiple pressures.^{28,29} However, given the complexity of plant-microbial interaction and its dependence on environmental variables, optimizing the relationship of plant microbes to increase drought tolerance in agricultural facilities is still a challenge. Developing drought-resistant plant genotypes, seed processing, genetic changes, plant-growing microorganisms, plant fertilizers, and appropriate dissolved substances are management approaches to promote drought tolerance in various agricultural facilities. Therefore, it is essential to have a thorough understanding of the possible improvement that can be attributed to plant-associated microbiomes on the production of agricultural plants as a mitigating technique for drought stress circumstances.

Drought Stress Effect on Plant Development

Drought is a period without rainfall, resulting in a considerable decrease in soil and relative humidity and a rise in atmospheric temperature.^{30,31} A mismatch between water input and soil steam flow can result in drought conditions. Plant health is directly and indirectly affected by drought stress. The penetration and ion balance of plant cells are affected by reducing the water availability of the roots and the loss of liquid during evapotranspiration, which leads to changes in the plant condition.³² It also affects crop growth in various ways, like slowing down seed germination, which negatively impacts on crop yield. Drought is the primary principal abiotic stress that influences morphological, biochemical, physiological, and molecular reactions by affecting the activity of proteins in drought stress; drought stress can damage the morphology, biochemistry, and physiology of wheat plants.³³ Drought substantially influences leaf size, plant height, and crop development owing to silk division, reduced cell growth, and elongation of photosynthesis because the decline in leaf growth and leaves' reduces the early stages of photosynthesis, thereby reducing the loss of food production. According to published studies, all essential activities, under drought stress, several processes, such as pure photosynthesis, the generation of photosynthetic pigments, electron transfer rates, the quantum efficiency of photosystem II, also known as PSII, is a crucial part of plants, algae, and some bacteria's photosynthetic machinery. It consists of proteins, pigments, and cofactors that absorb light energy and convert it into chemical energy. The main pigment is chlorophyll a, which maximizes photosynthesis efficiency. The energy is then excited in a reaction center, facilitating the synthesis of ATP and the reduction of NADP⁺ to NADPH. Photosystem II also plays a role in water splitting through photolysis, releasing oxygen and contributing to the oxygen-rich atmosphere. Understanding this system is vital for bioenergy research, plant biology, and environmental studies (II optical systems (PSII), protein synthesis, lipids, and energy metabolism, are suppressed.^{34,35} Drought prevents plant growth by disrupting the plant's water balance, membrane permeability, mineral nutrition, and enzyme activity, which substantially influence plant growth.³⁶

Drought pressure indirectly increases the production of ROS, which causes oxidative damage to the macromolecules.³⁷ Reactive oxygen species production leads to lipid oxidation, which causes damage to the membrane, enzyme inactivation, and structural and functional degradation of proteins. Protein oxidation and oxidative stress may result in the loss of enzyme activity and the creation of protease anticonvergent clumps. Therefore, plants often use various techniques to reduce ROS-mediated damage, such as the production of low molecular weight enzymes and zinc-free antioxidants. Other enzymes in the ascorbate-glutathione cycle, such as monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and GR, function to prevent dangerous oxygen derivatives from forming.³⁸

Various Techniques to the Amelioration of Drought Stress on Plants

Drought-resistant approaches have been demonstrated in a variety of studies, including (1) plant breeding and marker-assisted selection³⁹; (2) exogenously administered substances and osmolytes, such as polyols, glycine, betaine, proline, or other amino acids (sorbitol, pinitol, myoinositol, and mannitol), among others improve osmotic adjustment⁴⁰; (3) hormones produced by plants are (salicylic acid [SA], auxins, gibberellic acids [GAs], cytokinins [CKs], brassinosteroids [BRs], jasmonic acid [JA], and abscisic acid [ABA])⁴¹; and (4) antioxidant function (glutathione, polyamines, ascorbate, and enzymes)⁴². In the following subsections, we shall further dwell on some of the strategies to ameliorate drought stress.

Impact of phytohormones

Phytohormones play a crucial role in controlling plant responses to different types of drought. Plant hormones such as SA, JA, auxin, indole-3-acetic acid (IAA), ethylene (ET), CKs, BRs, and GAs are also needed for plants responsiveness to abiotic stresses.⁴³ The balance of auxin and CK, which regulates root growth and determines RSA, is a potent regulator of the plant organogenesis.⁴⁴ The endogenous ratio of auxin to CK in plants may be influenced by auxin and CK synthesis by rhizospheric bacteria and microbial metabolites that interact with these hormonal pathways. Low IAA levels may promote parent root elongation, while high IAA levels stimulate lateral root formation, root hair synthesis, and parent root growth.⁴⁵ Likewise, rice endophyte *Phomopsis liquidambari* B3 inoculation dramatically increased auxin, CK, and ET levels in rice at varied nitrogen levels.⁴⁶ *Azospirillum brasilense* also contains nitrite reductase activity and creates nitric oxide during root colonization, which mediate auxin signaling pathway to control the growth of LR.⁴⁷ Plant growth has been boosted by inoculating them with CK-producing rhizospheric bacteria.⁴⁸ Absciscic acid and GA, or substances that govern the concentration of these phytohormones in plants, are produced by rhizospheric bacteria, according to many studies.^{49,50} Rice root elongation is influenced by GAs, notably GA₃, which affects local auxin production and the polar auxin transport.⁴⁸ Indole butyric acid (IBA) therapy has been shown to help mung bean seedlings overcome root development inhibition.⁵¹ Surprisingly, rhizobacteria reduce drought-induced yield loss in plants by increasing auxin levels.^{52,53} Drought resistance is conferred by overexpression of sweet potato auxin response factor (ARF)5 in *Arabidopsis* through altering carotenoid biosynthesis, which is a precursor of IAA.⁵⁴ The co-expression of GA REQUIRING-5 (GA5) and DREB1A in *Arabidopsis* significantly increased drought tolerance without compromising growth or yield.⁵⁵

Drought triggers the production of the phytohormone ABA. Plant roots create ABA, which is then transferred to the leaves and used to regulate the stomatal aperture, SA and JA, in addition to ABA, are essential in the drought stress response. In addition, during drought, genes producing JA and SA are

downregulated in the sweet sorghum.⁵⁶ Salicylic acid is a non-enzymatic antioxidant that helps remove ROS from the body. Salicylic acid-related gushing signals influence microorganisms' whole-body resistance in the root and microbial selection mediated by host plants.⁵⁶ Sunflower (*Helianthus annuus*) phytoremediation and drought tolerance improve when PGPR and SA are used in combined form.^{57,58} Methyl jasmonate (MeJA) function in enhancing drought stress tolerance has been explored in 5 different wheat growers, and it was discovered that MeJA efficiently mitigates the negative effects of drought stress.^{59,60} In stressed plants, glutathione is engaged in a variety of physiological tasks, including the elimination of toxic ROS and metal detoxification. Drought-induced oxidative stress can be reduced by combining seed and foliar treatments with MeJA (20M) + SA (2mM), which controlled ABA and osmolytes levels as well as antioxidant enzyme activity.⁶¹

Impact of nanoparticles in the mitigation of drought stress

Due to the large surface area, varied pore size, and amorphous nature, nanoparticles (NPs) are very reactive. The contents of NPs are discharged from the organelles of plants.⁶² Antioxidant enzymes, which include CAT, SOD, peroxidase, APX, and others, are regulated by them. Drought, heat, cold, salt stress, and heavy metal toxicity may all be reduced by silicon-based nanoparticles (SNPs).⁶³ Stress alleviation strategies include (1) plant antioxidant defense mechanisms are activated; (2) coprecipitation of Si with dangerous metal ions; (3) immobilization of hazardous metal ions in the growth medium; and (4) absorption and compartmentation of metal ions inside plants. Linh et al⁶⁴ discovered that metal-based (copper, iron, cobalt, and zinc oxide) NPs may improve soybean drought tolerance by increasing relative water content, biomass reduction rate, and drought tolerance index. Seed germination (%) and total germinate rate are improved by zinc oxide NPs have suggested the efficacy of ZnO NPs in using seed reservoirs for seedling development and drought stress tolerance.⁶⁵ Researchers employed chitosan NPs to change biochemistry and gene expression in *Catharanthus roseus* (L) to increase drought stress resistance.⁶⁶⁻⁶⁸

Exogenously administered chemicals in the alleviation of drought stress

To address global issues in agricultural activities, research must focus on the enhancement and application of exogenous hormones, and the establishment of crop management systems to promote the efficiency of water usage.^{93,94} Reactive oxygen species is a vital deliverable that can lead to oxidation signal conduction, systemic acquired resistance (SAR), and systemic acquired adaptation (SAA) corresponding to exculfactors. Under pressure, oxidation signal conduction causes a series of protective responses and yield management. Plant ROS (superoxide and hydrogen peroxide) oxidizing enzymes interact and are found in various

Table 1. The involvement of osmolytes and phytohormones, and the interactions with some other chemicals in reducing drought stress in various plants.

CHEMICALS AND MIXTURES OF SUBSTANCES	CHEMICALS USED AND THEIR DOSAGES	SPECIES OF PLANTS	USEFUL RESOURCE	PROCEDURES OF IMPACT	REFERENCES
MeJA + SA	MeJA (20 μ M) and SA (2 mM)	Maize (<i>Zea mays</i> L)	Seed and foliar application	Drought-induced oxidative stress was prevented by regulating the levels of ABA and osmolytes, as well as the activity of antioxidant enzymes.	Tayyab et al ⁶¹
GA		Wheat	Foliar application	Glyoxalase I (Gly I) and glyoxalase II (Gly II) activities were stimulated to protect wheat seedlings from drought stress.	Al Mahmud et al ⁶⁹
GA and ABA		Tobacco		Stress tolerance, ROS scavenging, and carbon-nitrogen balance are all improved with this supplement.	Jakab et al ⁷⁰
BRs	0.01 μ M	<i>Brassica napus</i> , <i>Arabidopsis</i> , and rice	Seed application	CO ₂ assimilation and improved leaf water economy	Kagale et al ⁷¹ and Farooq et al ⁷²
MeJA	250 mg L ⁻¹	Citrus		Chlorophyll, sugar, and proline levels increased, whereas H ₂ O ₂ and O ₂ levels decreased dramatically.	Xiong et al ⁷³
JA + ABA	JA (100 μ M) and ABA (100 μ M)	Soybean		Managing trypsin inhibitors and alleviating the negative impacts of drought stress	Hassanein et al ⁷⁴
Spermidine (Spd)	0.5 mmol/L	White clover (<i>Trifolium repens</i> L)	Foliar application	Increased activity of antioxidant enzymes and promotion of the ascorbate-glutathione cycle	Li et al ⁷⁵
Proline		Rice	Foliar application	Antioxidant enzyme activity and GB concentration were increased, while lipid peroxidation was reduced.	Hanif et al ⁷⁶
Proline + SA	10 mM proline and 0.5 mM SA	Barley	Foliar application	Plant biomass, chlorophyll concentration, relative water content, antioxidant enzyme activity, and lipid peroxidation and hydrogen peroxide levels are all increased, while lipid peroxidation and hydrogen peroxide levels are reduced (H ₂ O ₂).	Abdelaal et al ⁷⁷
Proline + ABA	ABA (10 μ M) and 10 mM proline	Wheat	Foliar application	Drought and salinity stress tolerance has improved.	Kaur and Asthir ⁷⁸
Trehalose	(0 and 30 mM)	<i>Brassica</i> , Maize	Foliar application	Drought stress resistance was generated by increasing photosynthetic and water.	Ali and Ashraf ⁷⁹
				Relation properties, as well as antioxidant enzyme activity.	
	40 mM trehalose	Wheat	Foliar application	Wheat's physiological state is improved.	Ahmed et al ⁸⁰
	(0, 10, 20, and 30 mM)	Sunflower	Foliar application	Drought tolerance has been induced.	Kosar et al ⁸¹

(Continued)

Table 1. (Continued)

CHEMICALS AND MIXTURES OF SUBSTANCES	CHEMICALS USED AND THEIR DOSAGES	SPECIES OF PLANTS	USEFUL RESOURCE	PROCEDURES OF IMPACT	REFERENCES
Mannitol	30 mM	Blackgram (<i>Vigna mungo</i> L)	Foliar application	Osmotic adjustment and scavenge the stress-induced oxygen radicals	Dubey et al ⁸²
Mannitol + thiourea	M (15 and 30 mM) or T (3.5 and 7.0 mM)	Maize (<i>Zea mays</i> L)	Foliar application	Scavenge the stress induces oxygen radicals and osmotic adjustment.	Kaya et al ⁸³
GABA + Proline	GABA and proline (0, 0.25, 0.5, 0.75, and 1 mol/L)	Tobacco		Under drought stress, GABA functions as an effective osmolyte to minimize the generation of ROS.	Liu et al ⁸⁴
D-Ononitol		<i>Arabidopsis</i>		Prevent water loss in plants	Ahn et al ⁸⁵
D-pinitol		<i>Arabidopsis</i>		Prevent water loss in plants	Ahn et al ⁸⁶
GB	0, 50, 100, and 200 mM	<i>Phoebe hunanensis</i>	Foliar application	Improves cell membrane permeability and inhibits the buildup of membrane lipid peroxidase	Yang et al ⁸⁷
		Maize, barley		Maintaining photosynthetic efficiency, protecting the thylakoid membrane, and adjusting the osmotic pressure	Ashraf et al ⁸⁸
		Flax (<i>Linum usitatissimum</i>)	Foliar application	Enhanced antioxidative enzyme activity and increased osmolyte buildup	Gupta et al ⁸⁹
	(0, 50 and 100 mM)	Wheat	Foliar application	Under drought stress, increasing plant biomass, transpiration rate, and nitrogen and phosphorus concentration in roots	Shahbaz et al ⁹⁰
GB + SA	GB (100 mM) and SA (0.724 mM)	Sunflower	Foliar application	Drought boosted the concentration of free leaf proline and oil.	Hussain et al ⁹¹
GB + SA + zinc	11.5 g/L GB + 140 mg/L SA + 4 g/L Zn	Maize	Foliar application	Proline and sugar buildup, as well as antioxidative enzyme activity, have all improved.	Shemi et al ⁹²

Abbreviations: ABA, abscisic acid; JA, jasmonic acid; ROS, reactive oxygen species; MeJA, methyl jasmonate; SA, salicylic acid; GA, gibberellic acid; BRs, brassinosteroids; GABA, γ -amino butyric acid.

plant tissues. Glutathione has a combined effect on methylglyoxal detoxification and antioxidative enzyme production in water-stressed mung bean plants.⁹⁵ Through similar research, glutathione-mediated drought stress resistance was connected to enhanced ionic homeostasis and decreased oxidative stress in rice (*Oryza sativa* L).⁹⁶ Silicon is a valuable ingredient that helps mitigate the negative impacts of drought. Fortified fertilizers have lately sparked attention due to their various functions, including boosting plant growth, photosynthetic machinery, and preserving cellular ion homeostasis under stress.⁹⁷ Various silicon exporters have indeed been identified in the monocot and dicot plants.⁹⁸ Diamond et al⁹⁹ found that integrating Si and Arbuscular mycorrhizal fungus (AMF) increased strawberry plant biomass by increasing water content, water consumption performance, antioxidant enzyme activity, photosynthetic rate, and notably zinc nutritional intake. Exogenous silicon treatment

reduces oxidative damage caused by abiotic stressors in *Brassica napus* L¹⁰⁰ and wheat plants⁹⁷ by enhancing antioxidant enzyme activity. Selenium supplementation can cause an accumulation of solutes in grown plants in water-stressed conditions, lowering oxidative stress. In addition, selenium therapy can promote plant growth and antioxidant formation as they age and maintain a healthy water balance, enabling them to withstand drought stress.¹⁰¹ Osmolytes come in a wide variety of sizes and shapes. Because of their cellular defense mechanisms against dehydration loss, osmoprotectants are also called osmolytes.

Microbiome-induced resistance to drought stress

The plant microbiome is made up of bacteria found in the rhizosphere, endosphere, and phyllosphere, as well as other plant-related components, which include nectar and

pollen.^{13,102} Plants produce a range of chemical compounds in their root exudate, which improves plant absorption, stimulates the development, and increases yield.^{103,104}

Drought-tolerant microbiome plant recruitment may have developed through generations of recurring drought responses, resulting in positive and stable plant-microbe relationships that benefit both the microbe and the host plant.^{105,106} Drought-stressed PGPMs can be studied to discover which microbial features are advantageous to plants. Bacteria that promote plant growth (PG) have been discovered to increase nutrient bioavailability in soils for root absorption,^{18,107} especially in areas where there has been a protracted period of drought.¹⁰⁸ Plant growth-promoting rhizobacteria have been intensively examined in various crops, including soybeans, for their ability to mitigate the negative impacts of drought stress,^{4,109,110} wheat,^{111,112} chickpea,^{12,113} maize,^{114,115} rice,¹¹⁶ and mung bean.^{117,118}

Drought resistance is provided through several PGP abilities, the well-studied of which is the enzyme 1-aminocyclopropane-1-carboxylate deaminase.

In *Vigna mungo* L and *Pisum sativum*, ACCd-producing bacteria were shown to be beneficial in decreasing the negative impacts of drought stress,^{119,120} maize,^{4,121} soybean,⁴ and *Capsicum annuum*.¹²² Plant endophytes that dwell in the spaces between cells have been discovered to help plants cope with drought stress by generating a range of mechanisms that enable them to grow even when stressed.^{123,124} Even though drought has a considerable impact on plant-associated microbial communities, drought-tolerant microbiota has a significant beneficial impact on the phenological development of stressed plants.^{125,126} As a consequence, endophytes are considered among the most effective and widely accessible bioinput to increase plant drought tolerance.⁴

Plants that are drought-stressed undergo various physiological, metabolic, and molecular changes, all of which are mediated or regulated by microbiota.

To deal with abiotic stress, endophytic microorganisms can serve as a source of several “protective” substances such as antioxidants, polysaccharides, and proline.¹²⁷

Stress tolerance seems to be conferred by microbial endophytes through the activation and modulation of stress-responsive genes, the production of metabolites that mitigate stress, and the production of ROS waste pickers.¹²⁸

Etesami and Maheshwari¹²⁵ found that enzymatic activity of SOD, CAT, and peroxidase was all higher in plants infected with beneficial microorganisms (ie, *Bacillus cereus*, *B subtilis*, and *Serratia* sp). Several enzymes have been reported to be responsible for the reduction in adverse effects of drought on plants, thus indicating that the species of bacteria might be used as tools to assist plants in dealing with drought stress and growing more effectively.^{129,130}

Endophytic bacteria that produce melatonin, on the contrary, result in prolonged impacts on plant endogenous melatonin quantity when they invade parts of the plant. Endophytes

have been shown to affect tissue osmoregulation, stomatal conductance regulation, and cell-wall elasticity maintenance, all of which help plants withstand drought.⁴

Using proteomic and metabolomic approaches, *P indica* colonization of moisture-stressed barley roots increased the formation of proteins that protect photorespiration, energy management, primary metabolism, transporters, and autophagy, and during drought.¹³¹ *P indica* increased the accumulation of proteins that protect photorespiration, energy management, primary metabolism, transporters, and autophagy.¹³¹ The modifications in the host's amino acid metabolism might explain the favorable impact of *P indica* invasion on autophagy in drought-stressed plants.¹³¹

A long-term answer to the challenge of food security under abiotic stress settings is to integrate microbiota with agricultural practices. Notwithstanding, using these microbes in the field necessitates addressing a variety of issues, such as agronomic systems, microbe establishment, microbial inoculant invasion of soil and plant, and biosynthesis of bioactive metabolites primary and secondary metabolites involved in plant growth regulation, all of which have been done under a variety of soil types, climatic condition, and genotype conditions.^{29,132,133}

Late embryogenesis abundant proteins. Late embryogenesis abundant (LEA) proteins have traditionally been detected in seeds, but they may also be found in the plant's other reproductive tissues. Absciscic acid or ecological stress cues such as drought, low temperature, and salt, among others, activate the gene. They may act as water-holding molecules in ion sequestration and help in the stability of membranes and proteins, according to certain hypotheses.¹³⁴ Late embryogenesis abundant proteins have been examined in diverse plants by several researchers,¹³⁵ barley,^{135,136} rice,¹³⁷ and wheat,¹³⁸ to determine their role in drought stress tolerance.

Heat shock proteins. Plants in the field are subjected to a variety of biotic and abiotic stressors.¹³⁹ Plants react to these challenges by maintaining transcriptional and translational control over several metabolic processes.¹⁴⁰ It requires a team of molecular chaperones, like heat shock proteins (HSPs), to unravel the genetically diverse biological stress pathways.¹⁴¹ Although HSPs are commonly overexpressed in plants reacting to abiotic stress, their functional involvement in stress tolerance has received little attention. *Arabidopsis thaliana* is an example of a plant,¹⁴² soybean,^{143,144} and rice.^{145,146} The function of these HSPs has been investigated. Two nuclear/cytosolic HSPs identified in soybeans, GmDjp1 and DNA, have been connected to the abiotic¹⁴⁴ and biotic¹⁴³ stresses Heat shock protein90s, also known as glucose-regulated protein 94 (GRP94), are ER proteins that are essential for drought stress tolerance in drought-tolerant plants. Overexpression of SoyBiPD (soybean BiPs), another ER-resident HSP70s known as BiPs, enhanced drought stress resistance in tobacco (luminal-binding proteins).

Profiling impact of the unculturable microbiome in drought stress tolerance. Droughts are predicted to be more prolonged, frequent, and severe in the future than they have been in the past. It requires the development of innovative and fast-accessible technologies for enhancing and restoring drought resistance in crops. Plants and other land animals should cope with the drought created by diurnal and seasonal water changes.^{147,148} Plants are built to fight, endure, and avoid drying circumstances by changing their root architecture and development, altering their physiology, and closing their stomata on their above-ground segments.¹⁴⁹ Owing a better knowledge of the complex mechanism and feedback between plants and their microbial partners before and after drought would undoubtedly pave the way for better drought resistance in agricultural production by using the rhizosphere microbiome. Several studies have revealed that during drought, the microbiome of the plant root alters in favor of a few chosen microbial taxa, displacing the bulk of other microbial lineages.^{150,151}

The increase in the number of genes involved in the breakdown of complex plant polysaccharides, indicating the development of oligotrophic bacteria, is mainly responsible for this change in microbial communities.¹⁰⁵ One reason for Gram-positive bacteria's development in dry environments is that they are metabolically more active and hardier than Gram-negative bacteria.¹⁰⁵ Furthermore, research has shown that this abundance is linked to the length and severity of the drought and that it is thought to vanish whether water is reintroduced to the root system promptly.¹⁰⁸

Recent advances in omic biology, such as metagenomics, proteomics, and metabolomics, have allowed scientists to group genomes, proteomes, and metabolomes from different environments to understand better soil and plant-microbial dynamics, structure, and function communities, including secondary metabolite biosynthesis and genes.^{99,152} This research would benefit genes, glucose and secondary metabolites, transport, and metabolic pathways linked to bacterial enrichment under drought. In addition, the information obtained will help in the discovery of genetic features associated with these bacterial populations. The usefulness of multiomic approaches in understanding microbial features under drought has been proven in many recent studies.¹⁵³ Researchers investigated the dynamics of iron metabolism in a drought-induced rhizosphere microbiome using metagenome-guided comparative genomics.^{9,154} They discovered a link between drought, iron metabolism, and the plant root microbiome.¹⁵⁴ Michaletti et al¹⁵⁵ looked at some of the critical metabolites that may be used to construct models that show the association between yield-related parameters and different metabolic pathways while analyzing the proteome and metabolomics of spring wheat leaf tissues. Researchers studied soybean's metabolomic and transcriptome profiles treated with melatonin throughout the grain filling stage under drought stress conditions via modifying secondary metabolite formation pathways.¹⁵⁶

Utilization of genome editing technologies and tools

The utilization of GE technologies and tools has revolutionized the field of genetics and has had a profound impact on various areas of research and applications.¹⁵⁷ Genome editing refers to the precise modification of an organism's DNA, allowing scientists to make targeted changes to specific genes or genetic sequences.¹⁵⁸ One of the most widely used GE technologies is CRISPR-Cas9. CRISPR-Cas9 is a versatile and efficient tool that uses a guide RNA molecule to direct the Cas9 enzyme to a specific DNA sequence, where it can make precise cuts or introduce desired changes. This technology has greatly simplified the process of GE and has made it more accessible to researchers across different disciplines. The utilization of GE technologies has opened up new possibilities in agriculture. Researchers are using these tools to develop crops with improved traits, such as increased yield, enhanced nutritional content, and resistance to pests, diseases, and environmental stresses.¹⁵⁹ Genome editing has the potential to accelerate the breeding process and reduce the time required to develop new crop varieties.¹⁶⁰ Genome editing technologies are also being used in basic research to study gene function and understand the underlying mechanisms of various biological processes.¹⁶¹ By selectively modifying genes in model organisms, scientists can gain insights into the roles of specific genes and their contributions to development, disease, and other biological phenomena.¹⁶² However, it is important to note that the utilization of GE technologies also raises ethical and societal considerations. The potential for off-target effects and unintended consequences of GE must be carefully evaluated and addressed.¹⁶³ There is an ongoing need for responsible and transparent governance to ensure that these technologies are used ethically and for the benefit of society.¹⁶⁴ It is challenging to decipher the processes behind the harm caused by drought stress for the development of drought-tolerant plant. As a result, introducing the desired drought stress-resistant traits into many crops will be simpler by using transgenic or GE technologies. CRISPR has emerged as a cutting-edge method for GE in plants, allowing them to generate desirable traits and boost crop output under abiotic stress situations (Figure 1).

CRISPR/Cas9 has been found in a range of crops lately, including bread wheat,^{165,166} potato,¹⁶⁷ and model plants including *Arabidopsis thaliana*¹⁶⁸ and rice.¹⁶⁹ Increased expression of a variety of transcription factors (TFs) and genes involved in drought stress signaling aids plants in accumulating various metabolites, signaling molecules, and osmolytes, increasing drought stress tolerance. Plant dryness is caused by sensitive (S) gene expression, which causes hormonal imbalance, increases the formation of ROS, and decreases antioxidant activity. The expression of TF genes may also be through GE. The AREB1 TF gene's promoter activity was enhanced in *Arabidopsis* using a modified Cas9 (dCas9) linked with the histone acetylation transferase domain. Through the positive regulation of drought-tolerant genes, the genome-edited lines

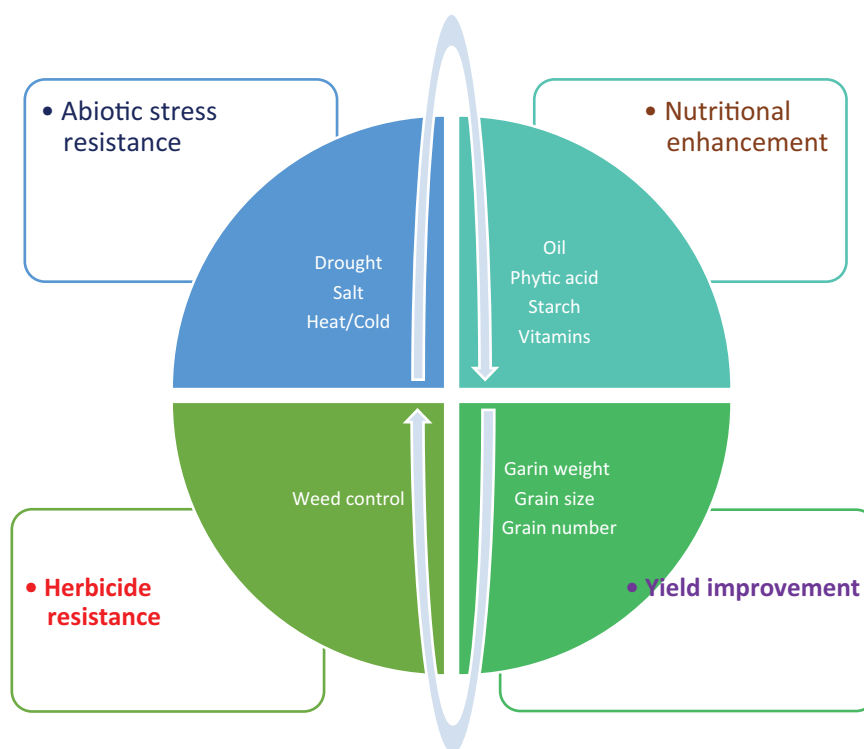


Figure 1. Utilization of genome modification tools and technologies.

demonstrated increased transcription of the AREB1 gene and acquired drought tolerance.¹⁷⁰ Plant genetic engineering has been transformed because of CRISPR technology's efficiency, resilience, and ease of engineering. The current status of this technology can revolutionize agriculture for improved crop production, increase crop resistance to biotic and abiotic challenges, and increase climate change resilience. Drought, heat, and salt are all abiotic stress elements that considerably impact crop output across the globe. Various complicated signaling networks regulate plant responses to stress stimuli. CRISPR technology's enhanced tools, such as base and prime editing, have considerably increased GE possibilities in agricultural plants without the requirement for DSBs.¹⁷¹ The CRISPR-Cas technology has opened up new possibilities in wheat research for improving grain quality. The TaGASR7 gene, linked to grain length, is part of the Snakin/GASA gene family.¹⁷² A CRISPR/Cas9 system that targeted TaGASR7 via the shoot apical meristem produced 11 mutant plants with desired alleles, and 3 plants passed the mutation down to the next cycle.¹⁷³ The TaGW2 gene, which encodes RING-type E3 ubiquitin ligase and is believed to be a negative regulator of wheat grain size and 1000-grain weight, was targeted using the CRISPR/Cas9 method. All 3 copies of the TaGW2 gene were mutated in the T1 knockout plant.^{174,175} Compared with wild-type plants, mutants exhibited dramatically enhanced attributes such as 1000-grain weight, grain area, grain breadth, and grain length. Wheat grains with a lower immunogenic response were obtained using CRISPR/Cas9 technology.¹⁷² The ARGOS family genes, specifically the Auxin-Regulated Gene Involved under Organ Size 8 (ARGOS8), block the ET

signaling pathway in drought circumstances resulting in increased yield and drought stress tolerance. In maize, on the contrary, endogenous expression of the ARGOS8 mRNA is very variable and low, according to the research.¹⁷⁶ Understanding gene function and the mutation necessary to bring about the desired change would be a key hurdle for successfully using CRISPR for crop improvement. It is worth noting that the targets and features generated using CRISPR are from functional research on model plants. CRISPR success must, however, be expanded to field crops to solve the issues of boosting food supply in the face of climate change. Similarly, in each plant species, genetic transformation processes are confined to a few genotypes referred to as "models." These plants often exhibit poor agronomic performance, like low yield, and are sensitive to several biotic and abiotic stressors. Introducing the CRISPR platform to field crops would save years of breeding time, but the barrier will remain a significant barrier to fully achieving the CRISPR promise.¹⁷⁷ Overall, these GE methods will open up new avenues for nucleotide-specific alterations. They may be actively researched in the future to enhance drought tolerance in crops, making them a powerful weapon for maintaining global food security.

Conclusions

Conclusively, the plant-associated microbiome has demonstrated potential qualities in reducing the stress caused by drought on agricultural plants. Improved drought resistance in plants may be a result of its capacity to increase water intake and retention, create stress protectants, and strengthen defense mechanisms against oxidative stress. It is crucial to remember

that the microbiome's efficacy might vary based on a number of circumstances. To fully use the potential of the plant-associated microbiome for sustainable agriculture and drought control, further study and knowledge of the individual microorganisms and their interactions with various plant species and environmental circumstances are required. Many strategies are needed to address the adverse effects of drought stress on agricultural plants, including PGPR and endophytes, seed lining with exogenous chemicals, growth hormones, biostimulants, and genetic modification. Using an omic approach that includes genomics, metabolomics, proteomics, and transcriptomics can help us better understand critical drought-tolerant genes and decipher complex signaling steps and gene structures associated with drought tolerance in many plants. Drought-tolerant products can be developed with the help of revolutionary methods like CRISPR/Cas9 GE tools, minimizing the global risk of food insecurity. Furthermore, learning more about the mechanisms through which soil microorganisms impact plant drought tolerance and recovery, as well as their interest and use in field situations, has a lot to say about increasing drought resistance in agricultural production systems. Novel treatments that incorporate physiological, molecular, and genetic methodologies would be advantageous to combat stress-related diseases.

Acknowledgements

VFA would like to thank the North-West University for the postgraduate doctoral bursary.

Author Contributions

VFA and OOB had the idea for the review article and suggested the review topic. VFA performed the literature search and wrote the first draft. OOB made substantial and technical contributions to the structure of the various manuscript drafts. Both authors read and approved the final manuscript.

ORCID iD

Olubukola Oluranti Babalola  <https://orcid.org/0000-0003-4344-1909>

REFERENCES

- Dubey A, Malla MA, Khan F, et al. Soil microbiome: a key player for conservation of soil health under changing climate. *Biodivers Conserv.* 2019;28:2405-2429.
- White JC, Gardea-Torresdey J. Achieving food security through the very small. *Nat Nanotechnol.* 2018;13:627-629.
- Dubey A, Kumar A, Abd_Allah EF, Hashem A, Khan ML. Growing more with less: breeding and developing drought resilient soybean to improve food security. *Ecol Indic.* 2019;105:425-437.
- Dubey A, Saiyam D, Kumar A, Hashem A, Abd_Allah EF, Khan ML. Bacterial root endophytes: characterization of their competence and plant growth promotion in soybean (*Glycine max* (L.) Merr.) under drought stress. *Int J Environ Res Public Health.* 2021;18:931.
- Chourasiya D, Agnihotri R, Prakash A, Pal KK, Sharma MP. Bioprotection of soybean plants from drought stress by application of bacterial and fungal endophytes. In: *Root Biology*. Springer; 2018; 15:101-140.
- Bedeke SB. Climate change vulnerability and adaptation of crop producers in sub-Saharan Africa: a review on concepts, approaches and methods. *Environ Dev Sustain.* 2023;25:1017-1051.
- Kokkanti RR, Vemuri H, Gaddameedi A, Rayalacheruvu U. Variability in drought stress-induced physiological, biochemical responses and expression of DREB2A, NAC4 and HSP70 genes in groundnut (*Arachis hypogaea* L.). *S Afr J Bot.* 2022;144:448-457.
- Baldoni E. Improving drought tolerance: can comparative transcriptomics support strategic rice breeding? *Plant Stress.* 2022;3:100058.
- Omotayo OP, Igiehon ON, Babalola OO. Metagenomic study of the community structure and functional potentials in maize rhizosphere microbiome: elucidation of mechanisms behind the improvement in plants under normal and stress conditions. *Sustainability.* 2021;13:8079.
- Fadiji AE, Babalola OO, Santoyo G, Perazzolli M. The potential role of microbial biostimulants in the amelioration of climate change-associated abiotic stresses on crops. *Front Microbiol.* 2022;12:829099.
- Umina PA, McDonald G, Maino J, Edwards O, Hoffmann AA. Escalating insecticide resistance in Australian grain pests: contributing factors, industry structure and management opportunities. *Pest Manag Sci.* 2019;75:1494-1506.
- Hashem A, Kumar A, Al-Dbass AM, et al. Arbuscular mycorrhizal fungi and biochar improves drought tolerance in chickpea. *Saudi J Biol Sci.* 2019;26:614-624.
- Dubey A, Kumar A, Khan ML. Role of biostimulants for enhancing abiotic stress tolerance in Fabaceae plants. In: *The Plant Family Fabaceae*. Springer; 2020.
- Ma S, Lv J, Li X, Ji T, Zhang Z, Gao L. Galactinol synthase gene 4 (*CsGolS4*) increases cold and drought tolerance in *Cucumis sativus* L. By inducing RFO accumulation and ROS scavenging. *Environ Exp Bot.* 2021;185:104406.
- Goswami A, Banerjee R, Raha S. Drought resistance in rice seedlings conferred by seed priming. *Protoplasma.* 2013;250:1115-1129.
- Zhang X, Liu X, Zhang D, et al. Genome-wide identification of gene expression in contrasting maize inbred lines under field drought conditions reveals the significance of transcription factors in drought tolerance. *PLoS ONE.* 2017;12:e0179477.
- Nadeem M, Li J, Yahya M, et al. Research progress and perspective on drought stress in legumes: a review. *Int J Mol Sci.* 2019;20:2541.
- Kumar A, Dubey A. Rhizosphere microbiome: engineering bacterial competitiveness for enhancing crop production. *J Adv Res.* 2020;24:337-352.
- Asmamaw M, Zawdie B. Mechanism and applications of CRISPR/Cas-9-mediated genome editing. *Biologics.* 2021;15:353-361.
- Prabhukarthikeyan SR, Parameswaran C, Keerthana U, et al. Understanding the plant-microbe interactions in CRISPR/Cas9 era: indeed a sprinting start in marathon. *Curr Genomics.* 2020;21:429-443.
- Yadav RK, Tripathi MK, Tiwari S, et al. Genome editing and improvement of abiotic stress tolerance in crop plants. *Life.* 2023;13:1456.
- Shahriar SA, Islam MN, Chun CNW, et al. Control of plant viral diseases by CRISPR/Cas9: resistance mechanisms, strategies and challenges in food crops. *Plants.* 2021;10:1264.
- Batista BD, Singh BK. Realities and hopes in the application of microbial tools in agriculture. *Microb Biotechnol.* 2021;14:1258-1268.
- Bruce A, Bruce D. Genome editing and responsible innovation, can they be reconciled? *J Agric Environ Ethics.* 2019;32:769-788.
- Jenkins D, Dobert R, Atanassova A, Pavely C. Impacts of the regulatory environment for gene editing on delivering beneficial products. *In Vitro Cell Dev Biol Plant.* 2021;57:609-626.
- Guo J, Muhammad H, Lv X, et al. Prospects and applications of plant growth promoting rhizobacteria to mitigate soil metal contamination: a review. *Chemosphere.* 2020;246:125823.
- Patil A, Gondi R, Rale V, Saroj SD. Microbial biofilms in plant disease management. In: *Biocontrol Mechanisms of Endophytic Microorganisms*. Elsevier; 2022.
- Gamalero E, Bona E, Glick BR. Current techniques to study beneficial plant-microbe interactions. *Microorganisms.* 2022;10:1380.
- Enebe MC, Babalola OO. The impact of microbes in the orchestration of plants' resistance to biotic stress: a disease management approach. *Appl Microbiol Biotechnol.* 2019;103:9-25.
- Mishra AK, Singh VP. A review of drought concepts. *J Hydrol.* 2010;391:202-216.
- Islam MS, Fahad S, Hossain A, et al. Legumes under drought stress: plant responses, adaptive mechanisms, and management strategies in relation to nitrogen fixation. In: *Engineering Tolerance in Crop Plants Against Abiotic Stress*. CRC Press; 2021.
- Giannakopoulos V. *Effects of Surfactant-Based Wetting Agents on Cereal Growth and Physiology*. Lancaster: Lancaster University; 2022.
- Siddique S, Naveed M, Yaseen M, Shahbaz M. Exploring potential of seed endophytic bacteria for enhancing drought stress resilience in maize (*Zea mays* L.). *Sustainability.* 2022;14:1-15.
- Tomar RS, Rai-Kalal P, Jajoo A. Impact of polycyclic aromatic hydrocarbons on photosynthetic and biochemical functions and its bioremediation by *Chlorella vulgaris*. *Algal Res.* 2022;67:102815.
- Li S, Li X, Ho S-H. How to enhance carbon capture by evolution of microalgal photosynthesis? *Sep Purif Technol.* 2022;291:120951.
- Bardhan K, Parekh VB, Jena S, More SJ, Padukkage D. Root system architectural and growth responses of crop plants to mineral nutrition under moisture

- stress and its implications in drought tolerance. In: *Climate Change and Crop Stress*. Elsevier; 2022.
37. Rajput S, Sengupta P, Kohli I, Varma A, Singh PK, Joshi NC. Role of Piriformospora indica in inducing soil microbial communities and drought stress tolerance in plants. In: *New and Future Developments in Microbial Biotechnology and Bioengineering*. Elsevier; 2022.
 38. Rasheed R, Ashraf MA, Ali S, et al. Role of NO in plants: a current update. In: *Nitric Oxide in Plant Biology*. Elsevier; 2022.
 39. Pérez-Méndez N, Miguel-Rojas C, Jimenez-Berni JA, et al. Plant breeding and management strategies to minimize the impact of water scarcity and biotic stress in cereal crops under Mediterranean conditions. *Agronomy*. 2022;12:75.
 40. Aftab T, Hakeem KR. *Plant Abiotic Stress Physiology: Volume 2: Molecular Advancements*. 2022.
 41. Chen H, Bullock DA, Alonso JM, Stepanova AN. To fight or to grow: the balancing role of ethylene in plant abiotic stress responses. *Plants*. 2022;11:33.
 42. Kaur G, Tak Y, Asthir B. Salicylic acid: a key signal molecule ameliorating plant stresses. *Cereal Res Commun*. 2022;50:617-626.
 43. Chapman KM, Marchi-Werle L, Hunt TE, Heng-Moss TM, Louis J. Absciscic and jasmonic acids contribute to soybean tolerance to the soybean aphid (*Aphis glycines* Matsumura). *Sci Rep*. 2018;8:1-12.
 44. Jing H, Strader LC. Interplay of auxin and cytokinin in lateral root development. *Int J Mol Sci*. 2019;20:486.
 45. Zhang G, Xu N, Chen H, Wang G, Huang J. OsMADS25 regulates root system development via auxin signalling in rice. *Plant J*. 2018;95:1004-1022.
 46. Li X, Zhou J, Xu R-S, Meng M-Y, Yu X, Dai C-C. Auxin, cytokinin, and ethylene involved in rice N availability improvement caused by endophyte *Phomopsis liquidambari*. *J Plant Growth Regul*. 2018;37:128-143.
 47. Rondina ABL, Dos Santos Sanzovo AW, Guimarães GS, Wendling JR, Nogueira MA, Hungria M. Changes in root morphological traits in soybean co-inoculated with *Bradyrhizobium* spp. *Azospirillum brasilense* or treated with *A. brasilense* exudates. *Biol Fertil Soils*. 2020;56:537-549.
 48. Li S-M, Zheng H-X, Zhang X-S, Sui N. Cytokinins as central regulators during plant growth and stress response. *Plant Cell Rep*. 2021;40:271-282.
 49. Wang R, Wang H-L, Tang R-P, et al. *Pseudomonas putida* represses JA- and SA-mediated defense pathways in rice and promotes an alternative defense mechanism possibly through ABA signaling. *Plants*. 2020;9:1641.
 50. Enebe MC, Babalola OO. The influence of plant growth-promoting rhizobacteria in plant tolerance to abiotic stress: a survival strategy. *Appl Microbiol Biotechnol*. 2018;102:7821-7835.
 51. Li SW, Zeng XY, Leng Y, Feng L, Kang XH. Indole-3-butyric acid mediates antioxidative defense systems to promote adventitious rooting in mung bean seedlings under cadmium and drought stresses. *Ecotoxicol Environ Saf*. 2018;161:332-341.
 52. Raheem A, Shaposhnikov A, Belimov AA, Dodd IC, Ali B. Auxin production by rhizobacteria was associated with improved yield of wheat (*Triticum aestivum* L.) under drought stress. *Arch Agron Soil Sci*. 2018;64:574-587.
 53. Aslam MM, Idris AL, Zhang Q, Weifeng X, Karanja JK, Wei Y. Rhizosphere microbiomes can regulate plant drought tolerance. *Pedosphere*. 2022;32:61-74.
 54. Kang C, He S, Zhai H, Li R, Zhao N, Liu Q. A sweetpotato auxin response factor gene (*IbARF5*) is involved in carotenoid biosynthesis and salt and drought tolerance in transgenic *Arabidopsis*. *Front Plant Sci*. 2018;9:1307.
 55. Kudo M, Kidokoro S, Yoshida T, et al. A gene-stacking approach to overcome the trade-off between drought stress tolerance and growth in *Arabidopsis*. *Plant J*. 2019;97:240-256.
 56. Varoquaux N, Cole B, Gao C, et al. Transcriptomic analysis of field-droughted sorghum from seedling to maturity reveals biotic and metabolic responses. *Proc Natl Acad Sci U S A*. 2019;116:27124-27132.
 57. Khan N, Zandi P, Ali S, Mehmood A, Adnan Shahid M, Yang J. Impact of salicylic acid and PGPR on the drought tolerance and phytoremediation potential of *Helianthus annuus*. *Front Microbiol*. 2018;9:2507.
 58. Adeleke BS, Ayangbenro AS, Babalola OO. Bacterial community structure of the sunflower (*Helianthus annuus*) endosphere. *Plant Signal Behav*. 2021;16:1974217.
 59. Parmoon G, Ebadi A, Hashemi M, Hawrylak-Nowak B, Baskin C, Jahanbakhsh S. Plant growth regulators improve grain production and water use efficiency of *Foeniculum vulgare* Mill. under water stress. *Plants*. 2022;11:1718.
 60. Awan SA, Khan I, Rizwan M, et al. Exogenous abscisic acid and jasmonic acid restrain polyethylene glycol-induced drought by improving the growth and antioxidative enzyme activities in pearl millet. *Physiol Plant*. 2021;172:809-819.
 61. Tayyab N, Naz R, Yasmin H, et al. Combined seed and foliar pre-treatments with exogenous methyl jasmonate and salicylic acid mitigate drought-induced stress in maize. *PLoS ONE*. 2020;15:e0232269.
 62. Rajput VD, Minkina T, Fedorenko A, et al. Effects of zinc oxide nanoparticles on physiological and anatomical indices in spring barley tissues. *Nanomaterials*. 2021;11:1722.
 63. Ali F, Bano A, Fazal A. Recent methods of drought stress tolerance in plants. *Plant Growth Regul*. 2017;82:363-375.
 64. Linh TM, Mai NC, Hoe PT, et al. Metal-based nanoparticles enhance drought tolerance in soybean. *J Nanomater*. 2020;2020:4056563.
 65. Ali EF, El-Shehawi AM, Ibrahim OHM, Abdul-Hafeez EY, Moussa MM, Hassan FAS. A vital role of chitosan nanoparticles in improvisation the drought stress tolerance in *Catharanthus roseus* (L.) through biochemical and gene expression modulation. *Plant Physiol Biochem*. 2021;161:166-175.
 66. Kandhol N, Jain M, Tripathi DK. Nanoparticles as potential hallmarks of drought stress tolerance in plants. *Physiol Plant*. 2022;174:e13665.
 67. Fadji AE, Mthiyane DMN, Onwudiwe DC, Babalola OO. Harnessing the known and unknown impact of nanotechnology on enhancing food security and reducing postharvest losses: constraints and future prospects. *Agronomy*. 2022;12:1657.
 68. Fadji AE, Mortimer PE, Xu J, Ebenso EE, Babalola OO. Biosynthesis of nanoparticles using endophytes: a novel approach for enhancing plant growth and sustainable agriculture. *Sustainability*. 2022;14:10839.
 69. Al Mahmud J, Biswas PK, Nahar K, Fujita M, Hasanuzzaman M. Exogenous application of gibberellic acid mitigates drought-induced damage in spring wheat. *Acta Agrobot*. 2019;72:1-18.
 70. Jakab G, Ton J, Flors V, Zimmerli L, Métraux JP, Mauch-Mani B. Enhancing *Arabidopsis* salt and drought stress tolerance by chemical priming for its abscisic acid responses. *Plant Physiol*. 2005;139:267-274.
 71. Kagale S, Divi UK, Krochko JE, Keller WA, Krishna P. Brassinosteroid confers tolerance in *Arabidopsis thaliana* and *Brassica napus* to a range of abiotic stresses. *Planta*. 2007;225:353-364.
 72. Farooq M, Wahid A, Basra S. Improving water relations and gas exchange with brassinosteroids in rice under drought stress. *J Agron Crop Sci*. 2009;195:262-269.
 73. Xiong B, Wang Y, Zhang Y, et al. Alleviation of drought stress and the physiological mechanisms in *Citrus* cultivar (Huangguogan) treated with methyl jasmonate. *Biosci Biotechnol Biochem*. 2020;84:1958-1965.
 74. Hassanein RA, Hassanein AA, El-Din AB, Salama M, Hashem HA. Role of jasmonic acid and abscisic acid treatments in alleviating the adverse effects of drought stress and regulating trypsin inhibitor production in soybean plant. *Aust J Basic Appl Sci*. 2009;3:904-919.
 75. Li Z, Peng Y, Zhang X-Q, et al. Exogenous spermidine improves water stress tolerance of white clover ("*Trifolium repens*" L.) involved in antioxidant defence, gene expression and proline metabolism. *Plant Omics*. 2014;7:517-526.
 76. Hanif S, Saleem MF, Sarwar M, et al. Biochemically triggered heat and drought stress tolerance in rice by proline application. *J Plant Growth Regul*. 2021;40:305-312.
 77. Abdelaal KA, Attia KA, Alamery SF, et al. Exogenous application of proline and salicylic acid can mitigate the injurious impacts of drought stress on barley plants associated with physiological and histological characters. *Sustainability*. 2020;12:1736.
 78. Kaur G, Asthir B. Impact of exogenously applied ABA on proline metabolism conferring drought and salinity stress tolerance in wheat genotypes. *Cereal Res Commun*. 2020;48:309-315.
 79. Ali Q, Ashraf M. 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*. 2011;197:258-271.
 80. Ahmed HE, Kord MA, Youssef H, Qaid EA. Exogenous application of trehalose improves the physiological status of wheat cv. Giza 168 grown under stress. *Egypt J Bot*. 2016;56:627-646.
 81. Kosar F, Akram NA, Ashraf M, Sadiq M, Al-Qurainy F. Trehalose-induced improvement in growth, photosynthetic characteristics and levels of some key osmoprotectants in sunflower (*Helianthus annuus* L.) under drought stress. *Pak J Bot*. 2018;50:955-961.
 82. Dubey A, Kumar A, Malla MA, et al. Approaches for the amelioration of adverse effects of drought stress on crop plants. *Front Biosci*. 2021;26:928-947.
 83. Kaya C, Sonmez O, Aydemir S, Ashraf M, Dikilitas M. Exogenous application of mannitol and thiourea regulates plant growth and oxidative stress responses in salt-stressed maize (*Zea mays* L.). *J Plant Interact*. 2013;8:234-241.
 84. Liu C, Zhao L, Yu G. The dominant glutamic acid metabolic flux to produce γ -amino butyric acid over proline in *Nicotiana tabacum* leaves under water stress relates to its significant role in antioxidant activity. *J Integr Plant Biol*. 2011;53:608-618.
 85. Ahn C, Park U, Park PB. Increased salt and drought tolerance by D-ononitol production in transgenic *Arabidopsis thaliana*. *Biochem Biophys Res Commun*. 2011;415:669-674.
 86. Ahn C-H, Hossain MA, Lee E, Kanth BK, Park PB. Increased salt and drought tolerance by D-pinitol production in transgenic *Arabidopsis thaliana*. *Biochem Biophys Res Commun*. 2018;504:315-320.
 87. Yang Y, Huang C, Ge Z, et al. Exogenous glycine betaine reduces drought damage by mediating osmotic adjustment and enhancing antioxidant defense in *Phoebe huanensis*. *Phyton*. 2022;91:129-148.

88. Ashraf M, Akram N, Al-Qurainy F, Foolad MR. Drought tolerance: roles of organic osmolytes, growth regulators, and mineral nutrients. *Adv Agron.* 2011;111:249-296.
89. Gupta P, Rai R, Sujata V, Yadava DK, Dash PK. Ex-foliar application of glycine betaine and its impact on protein, carbohydrates and induction of ROS scavenging system during drought stress in flax (*Linum usitatissimum*). *J Biotechnol.* 2021;337:80-89.
90. Shahbaz M, Masood Y, Perveen S, Ashraf M. Is foliar-applied glycinebetaine effective in mitigating the adverse effects of drought stress on wheat (*Triticum aestivum* L.)? *J Appl Bot Food Qual.* 2012;84:192.
91. Hussain M, Malik M, Farooq M, Ashraf M, Cheema M. Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. *J Agron Crop Sci.* 2008;194:193-199.
92. Shemi R, Wang R, Gheith E-SM, et al. Effects of salicylic acid, zinc and glycine betaine on morpho-physiological growth and yield of maize under drought stress. *Sci Rep.* 2021;11:1-14.
93. Anjum SA, Tanveer M, Hussain S, et al. Exogenously applied methyl jasmonate improves the drought tolerance in wheat imposed at early and late developmental stages. *Acta Physiol Plant.* 2016;38:25.
94. Li L, Gu W, Li C, et al. Exogenous spermidine improves drought tolerance in maize by enhancing the antioxidant defence system and regulating endogenous polyamine metabolism. *Crop Pasture Sci.* 2018;69:1076-1091.
95. Nahar K, Hasanuzzaman M, Alam M, Fujita M. Glutathione-induced drought stress tolerance in mung bean: coordinated roles of the antioxidant defence and methylglyoxal detoxification systems. *AOB Plants.* 2015;7:plv069.
96. Sohag AAM, Tahjib-Ul-Arif M, Polash MAS, et al. Exogenous glutathione-mediated drought stress tolerance in rice (*Oryza sativa* L.) is associated with lower oxidative damage and favorable ionic homeostasis. *Iran J Sci Technol Trans Sci.* 2020;44:955-971.
97. Gong H, Zhu X, Chen K, Wang S, Zhang C. Silicon alleviates oxidative damage of wheat plants in pots under drought. *Plant Sci.* 2005;169:313-321.
98. Deshmukh RK, Vivasco J, Ramakrishnan G, et al. A precise spacing between the NPA domains of aquaporins is essential for silicon permeability in plants. *Plant J.* 2015;83:489-500.
99. Diamond S, Andeer PF, Li Z, et al. Mediterranean grassland soil C-N compound turnover is dependent on rainfall and depth, and is mediated by genomically divergent microorganisms. *Nat Microbiol.* 2019;4:1356-1367.
100. Hasanuzzaman M, Nahar K, Anee T, Khan M, Fujita M. Silicon-mediated regulation of antioxidant defense and glyoxalase systems confers drought stress tolerance in *Brassica napus* L. *S Afr J Bot.* 2018;115:50-57.
101. Hawrylak-Nowak B, Dresler S, Rubinowska K, Matraszek-Gawron R, Woch W, Hasanuzzaman M. Selenium biofortification enhances the growth and alters the physiological response of lamb's lettuce grown under high temperature stress. *Plant Physiol Biochem.* 2018;127:446-456.
102. Kumar A, Sharma S, Mishra S. Evaluating effect of arbuscular mycorrhizal fungal consortia and *Azotobacter chroococcum* in improving biomass yield of *Jatropha curcas*. *Plant Biosyst.* 2016;150:1056-1064.
103. Van Der Heijden MG, Hartmann M. Networking in the plant microbiome. *PLoS Biol.* 2016;14:e1002378.
104. Moe LA. Amino acids in the rhizosphere: from plants to microbes. *Am J Bot.* 2013;100:1692-1705.
105. Naylor D, Coleman-Derr D. Drought stress and root-associated bacterial communities. *Front Plant Sci.* 2018;8:2223.
106. Naylor D, DeGraaf S, Purdom E, Coleman-Derr D. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME J.* 2017;11:2691-2704.
107. Bruno LB, Anbuganesan V, Karthik C, et al. Enhanced phytoextraction of multi-metal contaminated soils under increased atmospheric temperature by bioaugmentation with plant growth promoting *Bacillus cereus*. *J Environ Manage.* 2021;289:112553.
108. Xu L, Naylor D, Dong Z, et al. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. *Proc Natl Acad Sci U S A.* 2018;115:E4284-E4293.
109. Kunert KJ, Vorster BJ, Fenta BA, Kibido T, Dionisio G, Foyer CH. Drought stress responses in soybean roots and nodules. *Front Plant Sci.* 2016;7:1015.
110. Orozco-Mosqueda MDC, Fadji AE, Babalola OO, Glick BR, Santoyo G. Rhizobiome engineering: unveiling complex rhizosphere interactions to enhance plant growth and health. *Microbiol Res.* 2022;263:127137.
111. Gontia-Mishra I, Sapre S, Sharma A, Tiwari S. Amelioration of drought tolerance in wheat by the interaction of plant growth-promoting rhizobacteria. *Plant Biol (Stuttgart).* 2016;18:992-1000.
112. Barnawal D, Bharti N, Pandey SS, Pandey A, Chanotiya CS, Kalra A. Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1/TaDREB2 expression. *Physiol Plant.* 2017;161:502-514.
113. Kumar M, Mishra S, Dixit V, et al. Synergistic effect of *Pseudomonas putida* and *Bacillus amyloliquefaciens* ameliorates drought stress in chickpea (*Cicer arietinum* L.). *Plant Signal Behav.* 2016;11:e1071004.
114. Danish S, Zafar-Ul-Hye M, Mohsin F, Hussain M. ACC-deaminase producing plant growth promoting rhizobacteria and biochar mitigate adverse effects of drought stress on maize growth. *PLoS ONE.* 2020;15:e0230615.
115. Sandhya V, Shrivastava M, Ali SZ, Prasad VSSK. Endophytes from maize with plant growth promotion and biocontrol activity under drought stress. *Russ Agric Sci.* 2017;43:22-34.
116. Saddique MAB, Ali Z, Khan AS, Rana IA, Shamsi IH. Inoculation with the endophyte *Piriformospora indica* significantly affects mechanisms involved in osmotic stress in rice. *Rice.* 2018;11:1-12.
117. Kumari S, Vaishnav A, Jain S, Varma A, Choudhary DK. Induced drought tolerance through wild and mutant bacterial strain *Pseudomonas simiae* in mung bean (*Vigna radiata* L.). *World J Microbiol Biotechnol.* 2016;32:4-10.
118. Martins SJ, Rocha GA, de Melo HC, et al. Plant-associated bacteria mitigate drought stress in soybean. *Environ Sci Pollut Res Int.* 2018;25:13676-13686.
119. Gamalero E, Glick BR. Recent advances in bacterial amelioration of plant drought and salt stress. *Biology.* 2022;11:437.
120. Saikia J, Sarma RK, Dhandia R, et al. Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of North-east India. *Sci Rep.* 2018;8:1-16.
121. Fadji AE, Galemelwe O, Babalola OO. Unravelling the endophytic virome inhabiting maize plant. *Agronomy.* 2022;12:1867.
122. Maxton A, Singh P, Masih SA. ACC deaminase-producing bacteria mediated drought and salt tolerance in *Capsicum annum*. *J Plant Nutr.* 2018;41:574-583.
123. Namwongsa J, Jogloy S, Vorasoot N, Boonlue S, Riddech N, Mongkolthanarak W. Endophytic bacteria improve root traits, biomass and yield of *Helianthus tuberosus* L. under normal and deficit water conditions. *J Microbiol Biotechnol.* 2019;29:1777-1789.
124. Dubey A, Malla MA, Kumar A, Dayanandan S, Khan ML. Plants endophytes: unveiling hidden agenda for bioprospecting toward sustainable agriculture. *Crit Rev Biotechnol.* 2020;40:1210-1231.
125. Etesami H, Maheshwari DK. Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: action mechanisms and future prospects. *Ecotoxicol Environ Saf.* 2018;156:225-246.
126. Hare PD, Cress WA, Van Staden J. Dissecting the roles of osmolyte accumulation during stress. *Plant Cell Environ.* 1998;21:535-553.
127. Ek-Ramos MJ, Gomez-Flores R, Orozco-Flores AA, Rodríguez-Padilla C, González-Ochoa G, Tamez-Guerra P. Bioactive products from plant-endophytic Gram-positive bacteria. *Front Microbiol.* 2019;10:463.
128. Lata R, Chowdhury S, Gond SK, White JF Jr. Induction of abiotic stress tolerance in plants by endophytic microbes. *Lett Appl Microbiol.* 2018;66:268-276.
129. Bogati K, Walczak M. The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy.* 2022;12:189.
130. Fadji AE, Ayangbenro AS, Babalola OO. Unveiling the putative functional genes present in root-associated endophytic microbiome from maize plant using the shotgun approach. *J Appl Genet.* 2021;62:339-351.
131. Ghaffari MR, Mirzaei M, Ghabooli M, et al. Root endophytic fungus *Piriformospora indica* improves drought stress adaptation in barley by metabolic and proteomic reprogramming. *Environ Exp Bot.* 2019;157:197-210.
132. Trivedi P, Mattupalli C, Eversole K, Leach JE. Enabling sustainable agriculture through understanding and enhancement of microbiomes. *New Phytol.* 2021;230:2129-2147.
133. Adeleke BS, Babalola OO. Meta-omics of endophytic microbes in agricultural biotechnology. *Biocatal Agric Biotechnol.* 2022;42:102332.
134. Yang F, Tang C, Antonietti M. Natural and artificial humic substances to manage minerals, ions, water, and soil microorganisms. *Chem Soc Rev.* 2021;50:6221-6239.
135. Magwanga RO, Lu P, Kirungu JN, et al. Characterization of the late embryogenesis abundant (LEA) proteins family and their role in drought stress tolerance in upland cotton. *BMC Genet.* 2018;19:1-31.
136. Kosová K, Vitámvás P, Prášil IT. Wheat and barley dehydrins under cold, drought, and salinity-what can LEA-II proteins tell us about plant stress response? *Front Plant Sci.* 2014;5:343.
137. Kamarudin ZS, Yusop MR, Ismail MR, et al. LEA gene expression assessment in advanced mutant rice genotypes under drought stress. *Int J Genomics.* 2019;2019:1-8.
138. Ali M, Gul A, Hasan H, et al. LEA proteins and drought stress in wheat. In: *Climate Change and Food Security with Emphasis on Wheat*. Elsevier; 2020.
139. Verma AK, Tamadaddi C, Tak Y, et al. The expanding world of plant J-domain proteins. *CRC Crit Rev Plant Sci.* 2019;38:382-400.
140. Kissoudis C, van de Wiel C, Visser RG, van der Linden G. Enhancing crop resilience to combined abiotic and biotic stress through the dissection of physiological and molecular crosstalk. *Front Plant Sci.* 2014;5:207.
141. Al-Whaibi MH. Plant heat-shock proteins: a mini review. *J. King Saud Univ Sci.* 2011;23:139-150.
142. Tamura K, Takahashi H, Kunieda T, Fuji K, Shimada T, Hara-Nishimura I. Arabidopsis KAM2/GRV2 is required for proper endosome formation and

- functions in vacuolar sorting and determination of the embryo growth axis. *Plant Cell*. 2007;19:320-332.
143. Liu JZ, Whitham SA. Overexpression of a soybean nuclear localized type-III DnaJ domain-containing HSP40 reveals its roles in cell death and disease resistance. *Plant J*. 2013;74:110-121.
 144. So H-A, Chung E, Lee J-H. Molecular characterization of soybean GmDjp1 encoding a type III J-protein induced by abiotic stress. *Genes Genom*. 2013;35:247-256.
 145. Ohta M, Wakasa Y, Takahashi H, Hayashi S, Kudo K, Takaiwa F. Analysis of rice ER-resident J-proteins reveals diversity and functional differentiation of the ER-resident HSP70 system in plants. *J Exp Bot*. 2013;64:5429-5441.
 146. Ohta M, Takaiwa F. Emerging features of ER resident J-proteins in plants. *Plant Signal Behav*. 2014;9:e28194.
 147. Schimel JP. Life in dry soils: effects of drought on soil microbial communities and processes. *Annu Rev Ecol Evol*. 2018;49:409-432.
 148. Becklin KM, Anderson JT, Gerhart LM, Wadgymar SM, Wessinger CA, Ward JK. Examining plant physiological responses to climate change through an evolutionary lens. *Plant Physiol*. 2016;172:635-649.
 149. Gupta A, Rico-Medina A, Caño-Delgado AI. The physiology of plant responses to drought. *Science*. 2020;368:266-269.
 150. Fitzpatrick CR, Copeland J, Wang PW, Guttman DS, Kotanen PM, Johnson MT. Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc Natl Acad Sci U S A*. 2018;115:E1157-E1165.
 151. Timm C, Carter K, Carrell A, et al. Abiotic stresses shift belowground *Populus*-associated bacteria toward a core stress microbiome. *mSystems*. 2018;3:e00070-17.
 152. Malla MA, Dubey A, Kumar A, Yadav S, Hashem A, Abd_Allah EF. Exploring the human microbiome: the potential future role of next-generation sequencing in disease diagnosis and treatment. *Front Immunol*. 2019;9:2868.
 153. Crandall SG, Gold KM, Jiménez-Gasco MDM, Filgueiras CC, Willett DS. A multi-omics approach to solving problems in plant disease ecology. *PLoS ONE*. 2020;15:e0237975.
 154. Xu L, Dong Z, Chiniquy D, et al. Genome-resolved metagenomics reveals role of iron metabolism in drought-induced rhizosphere microbiome dynamics. *Nat Commun*. 2021;12:1-17.
 155. Michaletti A, Naghavi MR, Toorchi M, Zolla L, Rinalducci S. Metabolomics and proteomics reveal drought-stress responses of leaf tissues from spring-wheat. *Sci Rep*. 2018;8:1-18.
 156. Cao L, Jin X, Zhang Y, Zhang M, Wang Y. Transcriptomic and metabolomic profiling of melatonin treated soybean (*Glycine max* L.) under drought stress during grain filling period through regulation of secondary metabolite biosynthesis pathways. *PLoS ONE*. 2020;15:e0239701.
 157. Adli M. The CRISPR tool kit for genome editing and beyond. *Nat Commun*. 2018;9:1911.
 158. Zhang Y, Massel K, Godwin ID, Gao C. Applications and potential of genome editing in crop improvement. *Genome Biol*. 2018;19:1-11.
 159. Zaidi SSEA, Mahas A, Vanderschuren H, Mahfouz MM. Engineering crops of the future: CRISPR approaches to develop climate-resilient and disease-resistant plants. *Genome Biol*. 2020;21:1-19.
 160. Begna T. Speed breeding to accelerate crop improvement. *Int J Agricultural Sci Food Technol*. 2022;8:178-186.
 161. Li H, Yang Y, Hong W, Huang M, Wu M, Zhao X. Applications of genome editing technology in the targeted therapy of human diseases: mechanisms, advances and prospects. *Sig Transduct Target Ther*. 2020;5:1.
 162. Bock C, Datlinger P, Chardon F, et al. High-content CRISPR screening. *Nat Rev Methods Primers*. 2022;2:8.
 163. Guo C, Ma X, Gao F, Guo Y. Off-target effects in CRISPR/Cas9 gene editing. *Front Bioeng Biotechnol*. 2023;11:1143157.
 164. Cath C. Governing artificial intelligence: ethical, legal and technical opportunities and challenges. *Philos Trans A Math Phys Eng Sci*. 2018;376:20180080.
 165. Liang Z, Chen K, Li T, et al. Efficient DNA-free genome editing of bread wheat using CRISPR/Cas9 ribonucleoprotein complexes. *Nat Commun*. 2017;8:1-5.
 166. Zhang Z, Hua L, Gupta A, et al. Development of an *Agrobacterium*-delivered CRISPR/Cas9 system for wheat genome editing. *Plant Biotechnol J*. 2019;17:1623-1635.
 167. Andersson M, Turesson H, Nicolai A, Fält AS, Samuelsson M, Hofvander P. Efficient targeted multiallelic mutagenesis in tetraploid potato (*Solanum tuberosum*) by transient CRISPR-Cas9 expression in protoplasts. *Plant Cell Rep*. 2017;36:117-128.
 168. Ryder P, McHale M, Fort A, Spillane C. Generation of stable nulliplex autopolyploid lines of *Arabidopsis thaliana* using CRISPR/Cas9 genome editing. *Plant Cell Rep*. 2017;36:1005-1008.
 169. Fang H, Meng Q, Xu J, et al. Knock-down of stress inducible OsSRFP1 encoding an E3 ubiquitin ligase with transcriptional activation activity confers abiotic stress tolerance through enhancing antioxidant protection in rice. *Plant Mol Biol*. 2015;87:441-458.
 170. Paixao J, Gillet F, Ribeiro T. Improved drought stress tolerance in *Arabidopsis* by CRISPR/dCas9 fusion with a histone acetyl transferase. *Sci Rep*. 2019;9:8080.
 171. Chennakesavulu K, Singh H, Trivedi PK, Jain M, Yadav SR. State-of-the-art in CRISPR technology and engineering drought, salinity, and thermo-tolerant crop plants. *Plant Cell Rep*. 2022;41:815-831.
 172. Bansal M, Jindal S, Wani SH, Ganie SA, Singh R. Genome editing and trait improvement in wheat. In: *Physiological, Molecular, and Genetic Perspectives of Wheat Improvement*. 2021:263-283.
 173. Hamada H, Liu Y, Nagira Y, Miki R, Taoka N, Imai R. Biolistic-delivery-based transient CRISPR/Cas9 expression enables in planta genome editing in wheat. *Sci Rep*. 2018;8:14422.
 174. Wang W, Pan Q, He F, et al. Transgenerational CRISPR-Cas9 activity facilitates multiplex gene editing in allopolyploid wheat. *CRISPR J*. 2018;1:65-74.
 175. Wang W, Simmonds J, Pan Q, et al. Gene editing and mutagenesis reveal inter-cultivar differences and additivity in the contribution of TaGW2 homoeologues to grain size and weight in wheat. *Theor Appl Genet*. 2018;131:2463-2475.
 176. Joshi RK, Bharat SS, Mishra R. Engineering drought tolerance in plants through CRISPR/Cas genome editing. *3 Biotech*. 2020;10:400-414.
 177. Ahmad N, Rahman MU, Mukhtar Z, Zafar Y, Zhang B. A critical look on CRISPR-based genome editing in plants. *J Cell Physiol*. 2020;235:666-682.