Journal of Crop Health (2025) 77:17
https://doi.org/10.1007/s10343-024-01090-9

REVIEW

Enhancing Crop Resilience to Drought and Salinity: the Potential Role of Extremophiles in Mitigating Food Insecurity in Sub-Saharan Africa

Timothy Sibanda[1] · **Ramganesh Selvarajan**[2,3] · **Barbara Reinhold-Hurek**[4]

Received: 1 October 2024 / Accepted: 2 December 2024 / Published online: 20 December 2024
© The Author(s) 2024

Abstract

Agriculture forms the cornerstone of food security across sub-Saharan Africa (SSA), serving as a fundamental pillar that sustains livelihoods, supports economic resilience, and underpins regional stability. This region's population is projected to reach 2.4 billion by the year 2050, which will increase its food demand by 60%. However, recurrent droughts, temperature extremes, and increasing soil salinity are emerging as threats to present and future food security as they restrict agricultural productivity. The biggest challenge facing the SSA region lies in finding ways to adapt its agricultural practices to climate change. This article explores the potential role of extremophile microorganisms in enhancing crop resilience to abiotic stress. Research has so far shown that extremophiles alleviate drought stress in plants by increasing the expression of an array of novel genes, including genes responsible for induced drought, heat and salt stress tolerance, increased production of enzymatic antioxidants, as well as increased production of plant growth promoting phytohormones. Importantly, research shows that (i) extremophile-induced plant growth promotion and stress alleviation is triggered by the presence the stressor (ii) phylogenetically diverse microorganisms isolated from different desert plants can induce stress tolerance in heterologous crop hosts. These findings raise hopes of proofing crops against climate change-induced drought stress and hence ensure food security. However, research on the role of extremophiles in agriculture in the SSA region still lags behind. There is need to build capacity in extremophile agricultural biotechnology in this region, primarily in the form of bioprospecting for isolates exhibiting strong plant growth promoting capabilities.

Keywords Climate change · Extremophiles · Food security · Abiotic stress · Plant growth promoting bacteria · Stress alleviation

Introduction

Climate Change and Its Impacts On Food Security in Sub-Saharan Africa

Weather and climate bear a significant impact on all sectors of the world's economies, from manufacturing, transport, finance, security, and agriculture (Warsame et al. 2022; Ayugi et al. 2022). The latter is the mainstay of sub-Saharan African (SSA) economies (Salahuddin et al. 2020), with over 80% of livelihoods dependent on rainfed agriculture (Calzadilla et al. 2013; Mubeng-Tshitaka et al. 2023). However, the impacts of climate change, primarily manifesting in recurrent droughts and heatwaves (Tadesse et al. 2008; Serdeczny et al. 2017; Pondi et al. 2022), have significant impacts on SSA household food security (Pondi et al. 2022; Ayugi et al. 2022). Drought is a climatic phenomenon characterised by prolonged periods of below average rainfall (Wilhite et al. 1985; Mekonen et al. 2020; Warsame

✉ Timothy Sibanda
timothy.sibanda@wits.ac.za

1 School of Molecular and Cell Biology, Faculty of Science, University of the Witwatersrand, P Bag 3, Wits 2050, Johannesburg, South Africa

2 Institute of Deep-Sea Science and Engineering (IDSSE), Chinese Academy of Sciences (CAS), Sanya, China

3 Department of Environmental Sciences, College of Agriculture and Environmental Sciences, University of South Africa, Florida Campus, South Africa

4 CBIB Centre for Biomolecular Interactions Bremen, Department of Microbe-Plant Interactions, Faculty of Biology and Chemistry, University of Bremen, Bremen, Germany

et al. 2022), above average growing season temperatures (Cairns et al. 2013; Gbegbelegbe et al. 2023), and higher than normal evapotranspiration rates (Wilhite et al. 1985; Bhaga et al. 2020). Combined, these factors lead to insufficient water for agriculture, human and animal consumption, industry, and general ecosystem functioning. The severity and duration of droughts vary widely, depending on climatic conditions, geography, and human activities (Gbegbelegbe et al. 2023). The worst droughts are usually experienced in the SSA region, southern Europe, south Asia, some parts of Australia, as well as southern and northern America (Mekonen et al. 2020). However, of these regions, the SSA region suffers the worst effects of drought owing to lack of climate change mitigation strategies (Ofori et al. 2021; Pondi et al. 2022; Gittard 2023), as well as its mostly tropical climate which is already characterised by high baseline temperatures (Cairns et al. 2013; Amjath-Babu et al. 2016; Lottering et al. 2021). Almost every year, one or more countries in the SSA region experience drought. For example, Bhaga et al. (2020) report that Mauritania experienced drought in 2011, Mali in 2015, Cote d'Ivoire and South Africa in 2018, Madagascar in 2019, and Lesotho in 2020, every time plunging millions of people in the respective countries in dire need for food assistance, besides livestock losses. Of all climate change related challenges experienced in SSA, climate change induced drought presents one of the greatest threats to food security in this region (Lottering et al. 2021; Shukla et al. 2021). Not only does drought result in starvation and loss of life, but also in mass migrations from affected areas, potentially fuelling conflict (Shukla et al. 2021; Gittard 2023; Di Falco et al. 2024).

The gradual worsening of climate change threatens agricultural productivity and viability as it increases both the intensity and frequency of environmental stresses such as temperature extremes, drought, and salinity (Selim et al. 2019; Santpoort 2020; Uzilday and Ganie 2023). These stresses present one of the most unprecedented challenges currently affecting agricultural production and negatively impacting on food security (Parida and George 2015; Selim et al. 2019). With exceptions to the Sahelian region where agriculture is dominated by the production of millet and sorghum (Arumugam et al. 2023), over half of the SSA region is characterised by a maize-based diet system (ten Berge et al. 2019; Cairns et al. 2021; Dossa and Miassi 2023; Gbegbelegbe et al. 2023). However, most maize varieties that are currently produced in SSA are highly unadopted to drought and heat stress, with data presented by Gbegbelegbe et al. (2023) showing that countries in Southern Africa, including Zimbabwe, Zambia, Mozambique, South Africa, Namibia, and Eswatini, have experienced both a reduction in maize harvest per hectare, as well as a reduction in the total land area committed to maize production as a result of recurrent droughts between the years 2000 and 2016. Additionally, drought has also been linked to a reduction in the quality of cereal grains produced (Ayugi et al. 2022). It is predicted that maize yields decline linearly by 1.7% under drought stress for every degree Celsius above 30 °C in SSA (Cairns et al. 2013). Dossa and Miassi (2023) observed that the average climatic temperatures in Togo rose from 27 °C in 1990 to 29 °C in 2020, whereas the average rainfall kept fluctuating. Overall, these conditions have caused Togo's maize output to decline, with the country becoming a net maize importer to plug the resultant food shortages. While climate change impacts are expected to intensify in the foreseeable future, it is projected that over 89% of maize producing areas in Central Africa will experience declines in maize output, with equivalent maize output decreases being expected in 85% of maize producing areas in West Africa, 29% in Southern Africa, and 32% in East Africa (Stuch et al. 2020). On the other hand, a decline in crop yield has been observed at soil salinity levels exceeding 5 dS/m, which is equivalent to 50 mM NaCl (Santos et al. 2023).

Paradoxically, the Sub-Saharan Africa (SSA) region is home to the world's fastest growing population which is projected to double in size by the year 2050 (Waha et al. 2013; Ezeh et al. 2020). Correspondingly, the region's aggregate food demand is projected to grow by 60% in order to feed the additional population (Akinbode et al. 2022). This shows the need for the adoption of climate smart agricultural approaches that are likely to minimise losses especially during moderate drought scenarios thereby ensuring food security. Some of the proposed coping mechanisms include breeding for drought and heat resilient crop varieties, promoting crop and diet diversification in communities highly dependent on maize, investing in infrastructure for rainwater harvesting, and investing in off-farm incoming generating ventures (Cairns et al. 2013; Gbegbelegbe et al. 2023). While these proposals are scientifically sound, some of them, including breeding and infrastructure development for rainwater harvesting are prohibitively expensive (Amjath-Babu et al. 2016), require long timeframes to produce the desired result, or are unavailable to the majority of the SSA population, particularly those residing in remote areas. As a result, governments in the SSA region mostly resort to providing food aid and school feeding programmes as a way of protecting their people from the effects of drought induced food shortages (Ayugi et al. 2022). Unfortunately, this approach is both unsustainable and open to abuse, with food aid sometimes being distributed along political lines, leaving those not affiliated to ruling governments at the risk of starvation. There is therefore need for the adoption of cost-effective and sustainable climate adaptative agricultural approaches that will leave the power to produce food in the hands of smallholder farmers, who already play a pivotal role in the food security of SSA (Stuch et al. 2020). One

such option includes the use of plant growth promoting microorganisms that foster crop resilience to multiple abiotic stresses (Alori et al. 2020), in particular drought and salinity stresses. These microorganisms include archaea, bacteria, fungi, and yeasts, whose roles in plant growth promotion include nutrient solubilisation and fixing, organic matter decomposition, exopolysaccharide secretion, as well as phytohormone and siderophore production (Naik et al. 2019). In particular, extremophilic microorganisms are emerging as a viable alternative to mitigate the deleterious impacts of the combined effect of drought, salinity, and higher climatic temperatures on crop production (Alori et al. 2020; Zenteno-Alegría et al. 2024). Microbial extremophiles are adapted to survive in extreme environmental conditions which are regarded as inhospitable to other life forms, including extremely hot conditions (thermophiles), extremely saline/salty conditions (halophiles), extremely arid conditions (xerophiles) (Sangeetha et al. 2016; Kochhar et al. 2022), among other conditions. Desert ecosystems offer a promising source of extremophiles for use in alleviating abiotic stresses as they are believed to harbour microorganisms that are highly tolerant to extremes of temperature, aridity, salinity, pH, and UV radiation (Eida et al. 2018; Mukhtar et al. 2019; Alsharif et al. 2020; Xie and Pathomaree 2021). Desert adapted extremophiles are either found in association with plants (rhizospheric, endophytic, and epiphytic), or can be isolated directly from the desert soil.

However, plant associated extremophiles possess the advantage of having co-evolved with plants, and provide hope of transferability between unrelated plant species, particularly from wild desert plants to cultivated crop species. According to Marasco et al. (2013), plants growing in arid environments select for microbial assemblages that are metabolically and physiologically adapted to drought, thereby determining the ecological services they receive, which ultimately improve their resistance to various abiotic stresses.

Plant-associated extremophiles have been reported from all three domains of life: archaea, bacteria, and eukarya, and of different phyla including Actinobacteria, Ascomycota, Bacteroidetes, Basidiomycota, Crenarchaeota, Euryarchaeota, Firmicutes and Proteobacteria (Nath Yadav 2017). Given that multiple extreme conditions can occur in desert microbial niches, the vast majority of desert microbes are classified as polyextremophiles (Yadav 2021). Use of polyextremophilic microorganisms as plant growth promoters is all the more suitable considering that plants, being sessile, are simultaneously exposed to different abiotic stresses for long periods of their lifespan (Bokhari et al. 2019). For better appreciation of the physiological and molecular mechanisms of microbial plant growth promotion and stress alleviation, the following section discusses plants' response to drought and salinity stress.

Molecular and Physiological Responses of Plants to Drought and Salinity Stress

When exposed to stresses such as drought and high temperature, plants undergo morphological, physiological, and biochemical changes meant to counter the stress (Ayang-

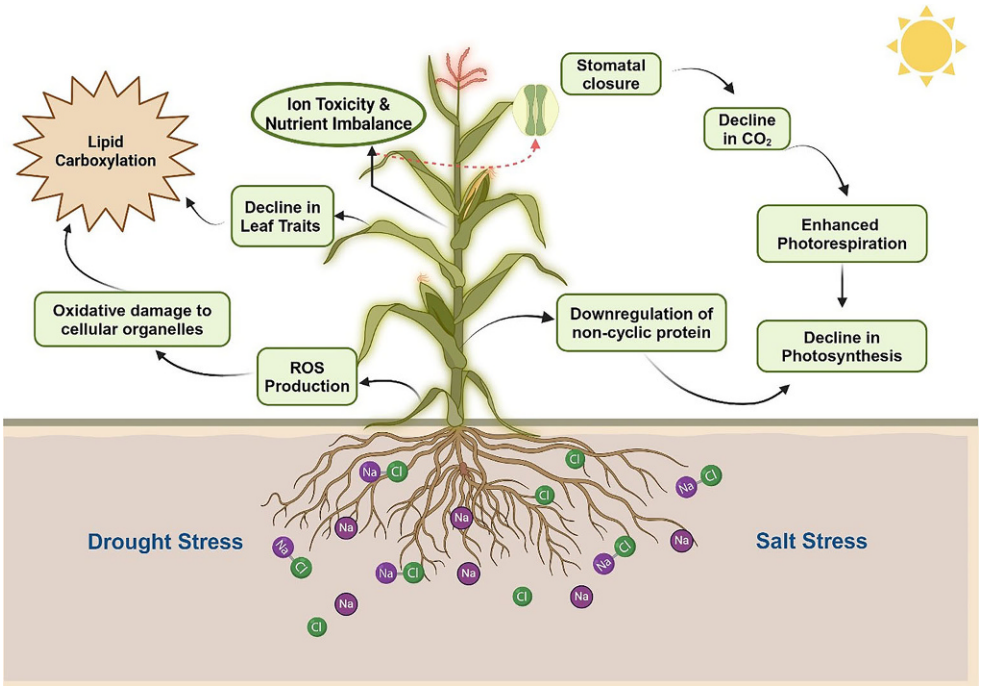

Fig. 1 Plant molecular and physiological response to drought and salinity stress (Figure created using Bio render Online tool)

benro and Babalola 2021). Some of these responses are shown in Fig. 1.

In a sustained drought scenario, plants undergo long-term physiological changes such as increased ethylene production in order to close stomata and so reduce transpirative water loss. However, ethylene levels inadvertently reach concentrations that block plant growth due to reduced photosynthetic rates as a result of decreased carbon dioxide uptake, as well as increasing root to shoot ratio in a bid to increase water uptake (Marasco et al. 2013). Additionally, the accumulation of reactive oxygen species (ROS) damages essential cellular molecules and structures including nucleic acids, proteins, and lipids, changing their configuration and hampering the overall survival of the plant (Kranner et al. 2008; Marasco et al. 2013). The higher-than-normal temperatures associated with drought conditions have been observed to stunt plant growth, reduce plants' ability to generate an immune response, as well as increase their susceptibility to virulence by pathogens (Xu and Weng 2020).

On the other hand, plants experience salt stress if there is excessive accumulation of water-soluble salts including calcium sulphate, magnesium chloride, magnesium sulphate, potassium sulphate, sodium nitrate, sodium chloride, sodium sulphate, and sodium carbonate (Gupta et al. 2022). The practice of irrigation, while used to sustain crop productivity during drought, has been implicated in increasing soil salinity levels due to the constant addition of irrigation water-borne dissolved salts (Chen et al. 2016; Santos et al. 2023). Plants exposed to the dual threat of drought and salt stress suffer from reduced photosynthetic activity owing to reduced gaseous exchange as stomata tend to close to reduce water loss, reduced nutrient metabolism, chlorophyll synthesis and ion uptake and translocation (Kaur and Asthir 2017; Hussain et al. 2018). Overall, whatever changes the plant undergoes under stress, it results in reduced survival, and ultimately productivity, which affects food security.

So far, the difficulty experienced by farmers in trying to adapt their farming practices to climate change is that under climate change, plants tend to concurrently experience a combined effect of multiple stresses such as drought, salinity and extreme heat, which complicates adaptation strategies. However, plant associated microbiomes in arid lands, in particular deserts, have been shown to promote multi-stress resilience to their host plants (Hnini and Aurag 2024). Therefore, their use as biofertilisers for climate adapted agriculture would have a distinct advantage stemming from the fact that most extremophiles are concurrently exposed to multiple stresses in their ecological niches, and

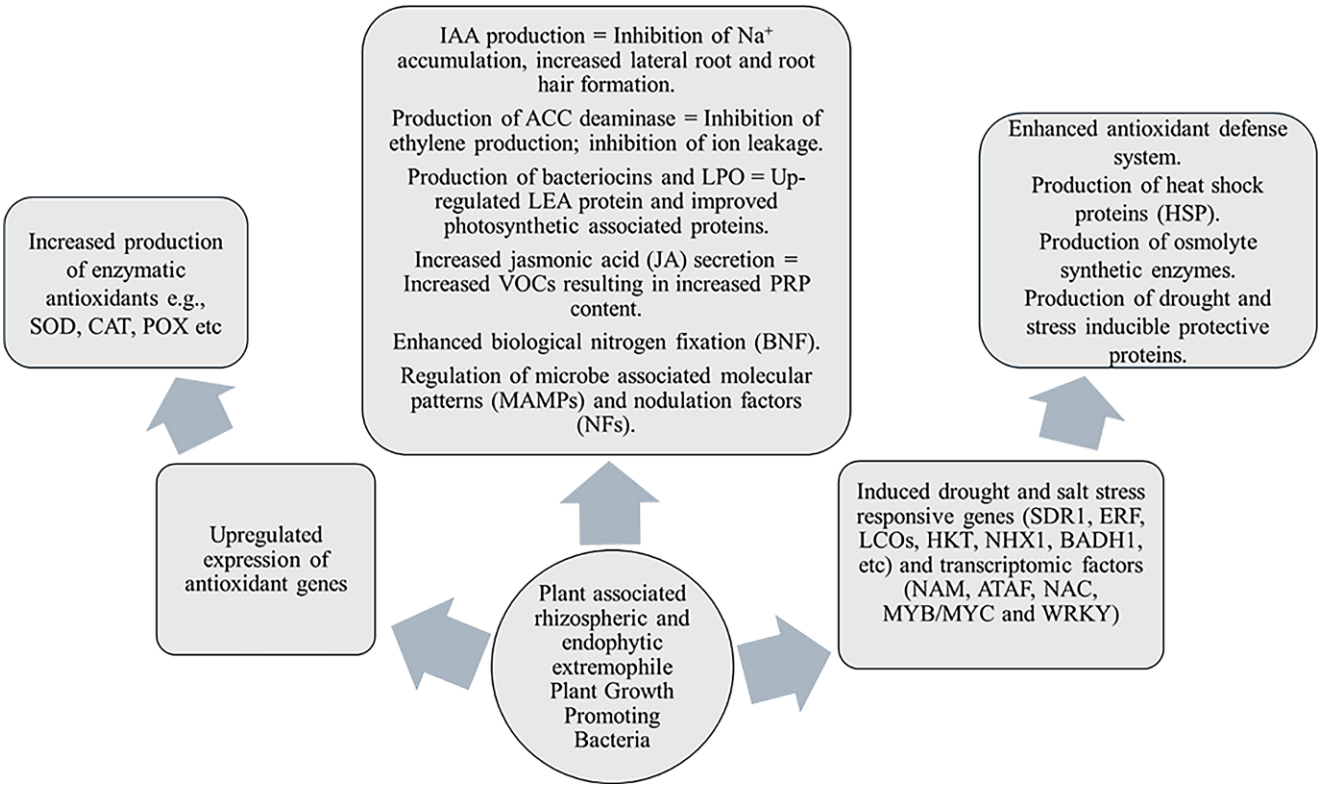

Fig. 2 Mechanisms of plant growth promoting bacteria-mediated drought and salinity stress tolerance in plants. *IAA* indole acetic acid; *SOD* superoxide dismutase; *CAT* catalase; *POX* peroxidases; *VOCs* volatile organic compounds; *SDR1* salt and drought responsive gene; *ERF* ethylene responsive element-binding factor; *LCOs* lipo-chitoolisaccharides; *HKT* high-affinity K^+ transporters; *NHX1* vacuolar Na^+/H^+ antiporter gene; *BADH1* betaine aldehyde dehydrogenase 1. Cited from Gupta et al. (2022), with modifications

so have evolved to be polyextremophiles. Their application to crops is therefore likely to foster crop resilience to the combined effects of drought, salinity, and heat, or to at least one of the stresses at a time. For example, some fungal endophytes isolated from desert grasses of the USA were observed to both alleviate drought stress in corn and cotton plants as well as to protect these plants from heat stress (Zenteno-Alegría et al. 2024). We discuss more on this in the following section.

Molecular and Physiological Mechanisms of Extremophile Induced Drought and Salinity Stress Alleviation in Plants

The potential with extremophiles lies in their ecological adaptation to extreme environments, which they find optimal for their physiological and ecological functions, aspects of which are important for promoting plant growth under hostile conditions (Santos et al. 2023). Extremophiles help plants combat drought conditions by increasing the expression of an array of novel genes (Fig. 2), including moisture-stress tolerance, phosphorus-solubilising genes, osmoregulatory genes, as well as decreasing catabolism (Parida and George 2015; Sangeetha et al. 2016; Andrés-Barrao et al. 2017; Kochhar et al. 2022).

These drought responsive genes are induced by endogenous abscisic acid (ABA), a phytohormone produced in plant roots and translocated to the rest of the plant in response to drought stress and increasing levels of ROS like hydrogen peroxide (H_2O_2), superoxide radical (O_2^-), and hydroxide radical (HO^-) (Kaur and Asthir 2017; Phillips and Ludidi 2017). However, extremophile production of ABA has been linked to increased drought stress tolerance in inoculated crops as compared to non-inoculated crops whose own ABA-mediated ROS scavenging activity is overwhelmed by ROS production at certain drought stress thresholds (de Carvalho 2008). Plant inoculation with extremophiles also results in increased expression of dehydration-inducible, osmoprotectants-producing genes

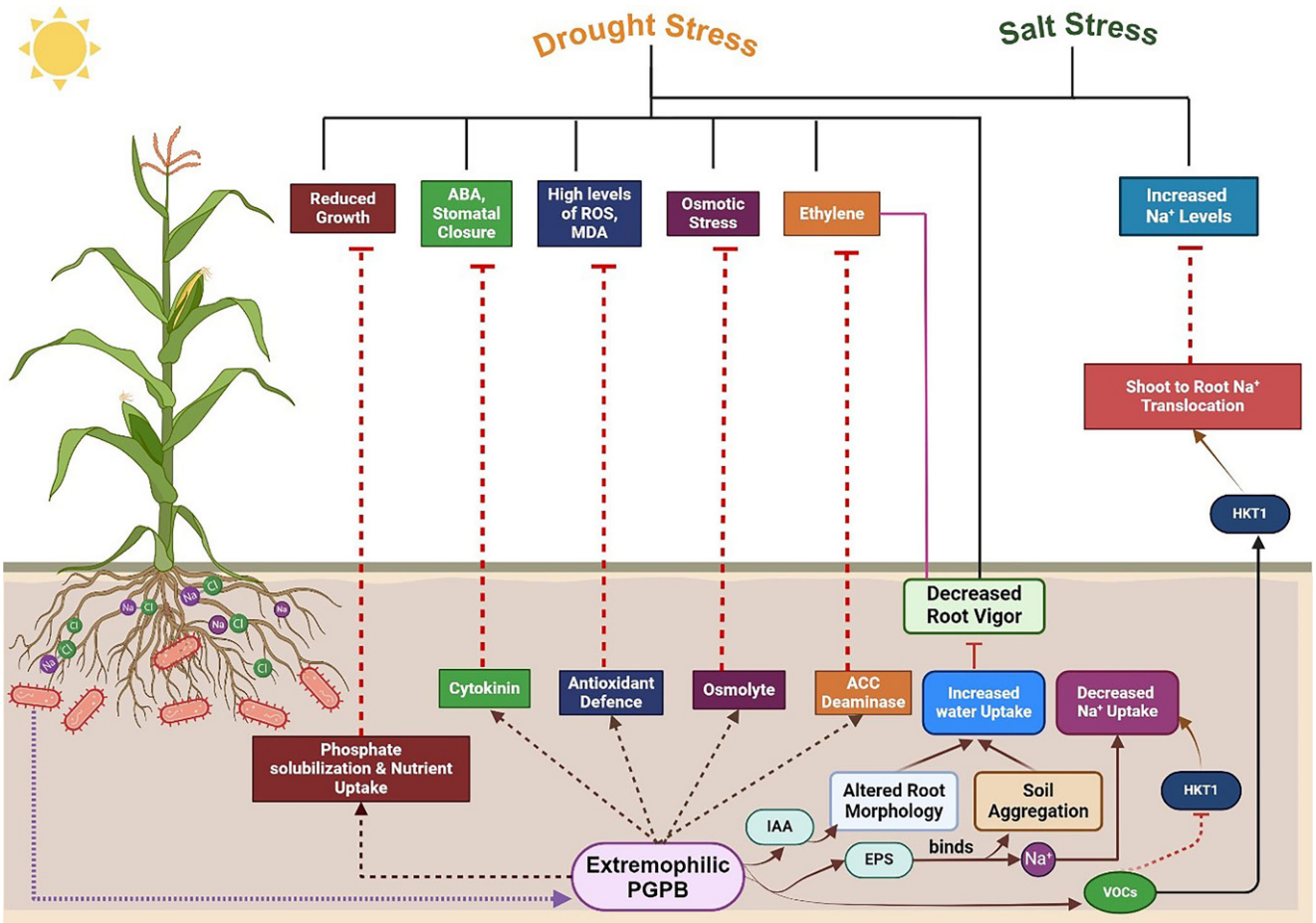

Fig. 3 A cascade of extremophile PGPB induced stimulation (↑) and inhibition () pathways that foster plant resilience to drought and salinity stress. *ACC deaminase* 1-aminocyclopropane-1-carboxylate deaminase, *IAA* indole-3-acetic acid, *EPS* exopolysaccharide, *VOCs* volatile organic acids, *MDA* malondialdehyde, *HKT1* High-affinity K+ transporter, *Na^+/H^+ antiporter* trafficking excess Na+ ions for elimination/sequestration. (Figure created using Bio render Online tool)

such as *AtBCAT2* (which codes for the enzyme branch-chain aminotransferase 2 responsible for the production of branched chain amino acids); *AtLKR/SDH* (codes for lysine ketoglutarate reductase/saccharopine dehydrogenase which produces saccharopine); *AtP5CS1*—delta 1-pyrroline-5-carboxylase 1 (produces proline), and *AtADC2*—arginine decarboxylase 2 (for production of agmatine) (Takahashi et al. 2020). Solutes like saccharopine, proline, and agmatine are known to perform a number of functions including lowering the water potential of plant cells thereby promoting plant water retention and maintenance of cell turgor for plant growth, protein stabilisation, as well as free radical scavenging activity thereby restoring cellular redox balance (Chun et al. 2018; Takahashi et al. 2020).

Further, and in a somewhat promising observation for microbially induced drought stress tolerance research involving crop plants, Marasco et al. (2013) revealed that bacteria-mediated drought resistance is not just a shared feature among different drought adapted bacterial species but is also transferable to different types of plants. Biomolecules produced by extremophiles within the plant rhizospheric region act as external stimuli when captured by sensors on plant cell membranes. Once received, the stimuli are transmitted through several signal transduction pathways to the nucleus, mediated by H_2O_2 as a secondary messenger molecule (de Carvalho 2008), resulting in the induction of drought-stress tolerance genes (Kaur and Asthir 2017). Other messenger molecules which play significant roles in signal transmitting pathways include Ca^{2+}, ROS, ABA, phosphoglycerol, diacylglycerol, and transcriptional regulators (Kaur and Asthir 2017). Overall, crop inoculation with extremophiles results in a cascade of pathways that result in abiotic stress alleviation as shown in Fig. 3.

As depicted in Fig. 3, 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing microbes degrade the ethylene precursor, ACC, into α-ketoglutarate and ammonia, thereby protecting the plant from the harmful effects of ethylene which the crop produces under drought stress (Rani et al. 2021). Degradation of ethylene restores normal plant growth under moisture stress conditions. Meanwhile, rhizospheric microbial extremophiles produce extracellular matrices favouring soil and water stability, increasing root adhering soil, and positively influencing water potential around the root system under drought conditions when limited water content causes salt accumulation, osmotic stress, and soil hardness. In addition, plant inoculation with extremophile PGPB promotes root development through the production of phytohormone-like substances like indole-3-acetic acid (IAA) (also called auxin) (Santos and Olivares 2021) leading to enhanced water and nutrient uptake, and therefore improved plant survival chances when water represents the limiting growth factor. Volatile organic compounds (VOCs) released by some microorganisms like *Bacillus subtilis* have been noted to stimulate plant biosynthesis of choline, a nutrient and solute involved in preventing water loss and eventual wilting by maintaining cell turgor pressure (Marasco et al. 2013). On the other hand, halophiles secrete haloenzymes with polyextremophilic features, including cellulases, xylanases, proteases, amylases, lipases, and gelatinases whose stable catalytic activities at elevated salt concentrations are crucially exploited by the plant for its own biochemical reactions (Munir et al. 2022), thereby fostering salt tolerance in these plants. Halophile microorganisms are divided into three categories according to their optimal sodium chloride (NaCl) requirements; slight halophiles (1–3%); moderate halophiles (3–15%), and extreme halophiles (15–30%) (Tuesta-Popolizio et al. 2021). As per Table 1 below, some species of these group were found to improve plant growth and enhance tolerance to salinity in some crops of agricultural interest like maize, wheat, rice, barley, oat, sunflower, and tomato. Overall, plant inoculation with extremophile microorganisms modulates plant molecular and physiological responses to both water deprivation and salinity stress as shown in Table 1, thereby increasing plant survival under adverse environmental conditions.

Research findings indicate that the plant growth promoting traits of extremophiles are stress-induced. For example, Inostroza et al. (2017) demonstrated that some halophiles significantly enhanced plant growth only under drought simulation and nutrient poor/rich soils as compared to well-watered, nutrient rich/poor soils. These observations are corroborated by Chen et al. (2017) who demonstrated that wheat plants inoculated with *Pantoea alhagi* exhibited significant differences in shoot and root length, as well as the total plant fresh weight between inoculated and uninoculated seedlings only when the inoculated seedlings were grown under simulated drought conditions. Similarly, Bokhari et al. (2019) observed that some *Bacillus* strains could not significantly influence *A. thaliana* growth under non-salt conditions, but significantly increased the fresh weight of the plant under salt stress conditions, when compared to the uninoculated control plants. Two important observations arising from these studies are: (1) the presence of the stressor, be it water deprivation, NaCl, or both, may be the trigger that induces extremophile microorganisms to produce factors that facilitate plant growth under stress conditions, and (2) phylogenetically diverse microorganisms isolated from different desert plants are able to induce stress tolerance in heterologous plant hosts, including cultivated crop plants through similar mechanisms as in the original host plants from which they were isolated. However, Bokhari et al. (2019) observed that while some *B. circulans* strains tested positive for PGP traits, they could not increase the growth of the target plant (*A. thaliana*) either under non-salt or under salt-stress

Table 1 Extremophile induced plant physiological responses to drought and salinity stress

Extremophile genera	Extremophile category	Inoculated crop	Microbe stress resilience	Observed growth promotion	Mode of action	References
Stenotrophomonas spp., *Exiguobacterium* spp.	Halophiles	Soybean	Growth at 1250–1500 mM NaCl	*Compared to uninoculated seeds/control plants:* Inoculated seed germination increased by between 35 to 43% Inoculated plant roots doubled in length and dry biomass under 250 mM NaCl	**Physiological:** Phosphate solubilisation, nitrogen fixation, and production of IAA and siderophores **Molecular:** Induction of plant salt stress responsive genes, including *Glyma.02G228100, Glyma.04G180400, Glyma.08G189600*, and *Glyma.17G173200*	Santos et al. (2023)
Bacillus safensis, Bacillus pumilus, Kocuria rosea, Enterobacter aerogenes, Aeromonas veronii	Halophiles	Maize	Not tested	*Compared to uninoculated control plants:* Inoculated crops showed significantly increased root and shoot growth Inoculations under salinity stress resulted in higher concentrations of osmolytes (proline, glycine betaine, and malondialdehyde) in maize leaf tissues, resulting in enhanced salinity stress tolerance	**Physiological:** Phosphate solubilisation, production of IAA and ACC deaminase **Molecular:** Not investigated	Mukhtar et al. (2020)
Pantoea sp.	Halophiles	*Vachellia tortilis* subsp. *Raddiana* (Sahara Desert tree)	Growth in media containing 10% polyethylene glycol (PEG, P6000) showed drought stress tolerance. Growth in 10% NaCl showed salt stress tolerance by	Increased root and shoot length	**Physiological:** Phosphate solubilisation and siderophore production. **Molecular:** Not investigated	Hnini and Aurag (2024)
Unidentified	Halophiles and haloalkaliphiles	*Prunus amygdalus* (almond)	Not determined	*Compared to uninoculated plant, inoculated plants exhibited:* More chlorophyll, sugar and proline Greater fresh and dry root and shoot biomass	**Physiological:** Phosphate solubilisation, and production of IAA and exopolysaccharides **Molecular:** Not investigated	Torbaghan et al. (2023)
Rhodotorula mucilaginosa, *Naganishia albida* (yeasts)	Halophiles	*Medicago sativa* (Alfalfa)	Tolerance to 2M NaCl (salt stress tolerance), and growth in medium containing 60% PEG exhibiting drought tolerance	Inoculated plants exhibited significantly increased number of leaves per plant, higher root and shoot biomass, as well as overall dry matter biomass compared to uninoculated plants	**Physiological:** Production of IAA, siderophores, and ACC deaminase **Molecular:** Not investigated	Raklami et al. (2024)
Klebsiella oxytoca, Citrobacter *freundii*	Halophiles	Pepper plants	Not investigated	Increasing root biomass by up to 40%, increasing plant tolerance to water deprivation Reduced decline in photosynthetic activity under drought stress, compared to uninoculated plants	**Physiological:** Production of volatile organic acids (VOCs), ACC deaminase, and IAA **Molecular:** Not investigated	Marasco et al. (2013)

Table 1 (Continued)

Extremophile genera	Extremophile category	Inoculated crop	Microbe stress resilience	Observed growth promotion	Mode of action	References
Pseudomonas frederickbergensis, Pseudomonas brassicacearum	Halophiles	Tunisian and Saudi Arabian Date palm and *Arabidopsis thaliana*	Isolates showed tolerance to drought, salt and temperature variation	Inoculated date palm plantlets displayed significantly higher aerial and root fresh biomasses compared to non-inoculated plants. Overall, inoculation significantly increased plant growth	**Physiological:** Phosphate solubilisation, nitrogen fixation, and production of IAA, siderophores, EPS, and ammonia **Molecular:** Not investigated	Cherif et al. (2015)
Pantoea alhagi	Halophile	Wheat	Isolates showed high temperature and salt stress tolerance by growing at 48 °C in tryptic soy broth, and in the presence of 9% NaCl, respectively	Inoculated seedlings showed significantly increased shoot, root and total plant fresh weight compared to uninoculated seedlings when deprived of water. Decreased degradation of chlorophyl	**Physiological:** Production of IAA and siderophores **Molecular:** Not investigated	Chen et al. (2017)
Streptomyces sp. (actinobacteria)	Arid tolerant	Maize	Not investigated	Plants inoculated with actinobacteria, and water stressed showed significant increases in fresh and dry weight compared to uninoculated control plants. Inoculated maize plants also exhibited increased photosynthesis under drought conditions compared to non-inoculated ones	**Physiological:** Production of IAA, siderophores, and gibberellic acid (GA) **Molecular:** Not investigated	Selim et al. (2019)
Bacillus endophyte strains	Halophile	*Arabidopsis thaliana* (mouse-ear cress)	Isolates could grow at 50 °C, and in medium containing 2M NaCl	Inoculated plants add significantly higher fresh weight when grown under salt stress conditions when compared to the uninoculated control plants	**Physiological:** Phosphate solubilisation, siderophore and IAA production **Molecular:** Not investigated	Bokhari et al. (2019)
Bacillus paralicheniformis, Pseudomonas lini	Halophile	*Arabidopsis thaliana, Cucumis sativus* (cucumber), and *Citrullus lanatus* (watermelon)	Isolates showed salinity stress by growing at 200 mM NaCl	Compared to uninoculated plants, inoculated plants had significantly increased root length, lateral root development, as well as root fresh weight when grown under salt stress (200 mM NaCl)	**Physiological:** Phosphate solubilisation, siderophore and IAA production **Molecular:** Not investigated	Palacio-Rodríguez et al. (2017)
Cellulomonas sp. *Arthrobacter* sp. *Microbacterium* sp. *Pantoea* sp. *Bacillus* sp.	Halophiles	*Arabidopsis thaliana*	Isolates exhibited drought and salinity stress by growing in media supplemented with 10% polyethylene-glycol (PEG, P8000) and 0.5 M NaCl respectively	Inoculated plants had significantly higher fresh and dry root biomass compared to uninoculated plants	**Physiological:** Production of IAA and ACC deaminase **Molecular:** Salt-stress induced expression of the K^+ *Transporter 1* (*AKT1*), *High-Affinity* K^+ *Transporter* (*HKT1-5*) and *Salt Overly Sensitive* (*SOS*) genes resulting in reduced plant Na^+ uptake and higher K^+ intake in inoculated plants compared to uninoculated plants	Eida et al. (2019)

Table 1 (Continued)

Extremophile genera	Extremophile category	Inoculated crop	Microbe stress resilience	Observed growth promotion	Mode of action	References
Stutzerimonas stutzeri *Bacillus pumilus*	Halophiles	*Medicago sativa* (Alfalfa plant) *Medicago polymorpha* (California burclover)	Isolates were able to grow in medium supplemented with 200 mM of NaCl	Inoculated seeds exhibited a reduced decline in germination compared to uninoculated plants under osmotic stress Inoculated plants had significantly increased root size under osmotic stress compared to uninoculated plants	**Physiological:** Nitrogen fixation, phosphate and potassium solubilisation, production of ACC deaminase, siderophores, and auxins **Molecular:** Not investigated	Gil et al. (2023)

conditions. This is an important observation in the process of biofertiliser research and development as it proves that until microorganisms are able to prove their PGP traits *in planta*, they may not necessarily be concluded as plant growth promoters based on their ability to demonstrate PGP traits *in vitro*.

At the molecular level, the stress-depended extremophile response leads to either the upregulation or downregulation of genes concerned with stress susceptibility, thereby increasing both plant growth as well as stress tolerance. For instance, the upregulation of osmoprotectants-encoding genes (e.g., proline and malondialdehyde (MDA)) in extremophile-inoculated plants under drought stress results in reduced oxidative damage of plant cellular structures (Andrés-Barrao et al. 2017). Similarly, Eida et al. (2019) describe a scenario where, inoculating *Arabidopsis thaliana* with halophilic bacteria endophytes resulted in the downregulation of the genes *AKT1, GORK, KUP6, SOS1* and *SOS3* in the shoots and an upregulation of the genes *HAK5, SKOR*, and *HKT1* in the roots. The general physiology of the Na^+-K^+ pump is such that the higher uptake of K^+ increases the efflux of Na^+, thereby maintaining the cell's osmotic pressure and cell integrity. The halophile-induced overexpression of the high-affinity plasma membrane Na^+/K^+ symporter *HKT1* leads to increased unloading/retrieval of Na^+ from the root xylem into the xylem parenchyma, ultimately leading to reduced Na^+ accumulation in the leaves, causing the plants to have higher salt tolerance. Further, Santos et al. (2023) linked the inoculation of soybean with *Stenotrophomonas* sp. to the upregulated expression of the salt stress tolerance soybean gene *Glyma.02G228100* (encodes for glutamine-dependent asparagine synthase 1 (ASN1)) under salt-stress conditions, thereby enabling the soybeans to thrive under salt stress.

Using a genome sequencing study, Andrés-Barrao et al. (2017) elucidated that an endophytic bacterium, *Enterobacter* sp., confers multi-stress tolerance to its host plants owing to a number of biosynthetic pathways and/genes that it contained. They discovered that the strain contained biosynthetic pathways for the production of osmoprotectants like proline as well as trehalose. Proline is a proteinogenic amino acid known to confer salt tolerance to organisms (Joanna et al. 2023). The strain also had pathways for membrane transporters like ProP whose role is in the uptake of osmoprotectants like carnitine. In nature, carnitine released into the rhizosphere by microbes can be assimilated by plants resulting in significantly higher osmotolerance than that afforded by proline under salt concentrations (Charrier et al. 2012; Oney-Birol 2019). The repertoire of stress-response biosynthetic pathways also included the cation/proton (H+) antiporters that contribute to osmoregulation; ABC transporters involved in the uptake of nutrients (e.g., phosphate, sulphate, nitrate, etc), and the

genes for siderophore enterobactin synthesis, plant defense to oxidative stress, as well as plant hormone modulation and growth promotion.

Numerous other studies, including Osman et al. (2016), Singh and Jha (2016) and Eida et al. (2018) have also confirmed both the plant growth promoting traits of desert plant associated rhizobacteria and endophytes, as well as their ability to confer salt stress tolerance onto cultivated crop plants. The common thread among all such research studies is that regardless of what plant the rhizobacteria/endophytes are isolated from, they are still equally capable of inducing stress resilience in other, non-related plants. Further, a study by Singh and Jha (2016) reports colonisation of wheat roots by *Serratia marcescens* in the range of 1.1×10^4 CFU/g of the root after 15 days of inoculation. This ability of the inoculum to colonise plant roots significantly enhances plant physiological and biochemical responses to abiotic stresses, allowing them to maintain critical metabolic activity. Finally, the tendency of the extremophiles to express their stress alleviating traits only in the presence of the stressor makes them invaluable resources for the formulation of biofertilisers for application in places affected by specific abiotic stresses. In conclusion of this section, is worth noting that some microorganisms associated with extreme environments represent a potentially vast repertoire of biofertilisers due to their ability to produce unique secondary metabolites and robust enzymes, making them suitable for supporting plant growth under abiotic stresses (Santos and Olivares 2021; Kochhar et al. 2022). They therefore have the potential to provide critical ecosystem services to farmers in drought prone areas like the sub-Saharan Africa (SSA) whose food security hangs in the balance owing to lack of climate adaptable agricultural practices.

Likely Role of Extremophiles in Agriculture in Sub-Saharan Africa

In light of the discussions in the above sections and taking into consideration the negative impacts of drought and soil salinity on the food security situation of SSA as highlighted in the introduction, the need for research that spearheads the adoption of extremophile based biofertilisers cannot be understated. In the Middle East, a project known as Darwin21 (https://www.darwin21.org/) has been launched with the aim to prospect different desert ecosystems for plant growth promoting rhizosphere microbes for application in organic and sustainable agriculture. The project has so far generated over 1500 culturable microbial strains from various deserts in the Middle East whose capacity to confer salt, drought and heat tolerance on both model and crop plants has been confirmed (Bang et al. 2018). Unfortunately, and despite its agricultural sector being severely affected by climate change induced recurrent droughts that threaten food security, not much research has been done in the SSA region to bioprospect for drought-adapted plant growth promoting microbes as a strategy for climate-change adapted agriculture. This is despite the region being home to a number of deserts from which samples could be obtained for the isolation of plant-associated extremophiles, including the 700 km^2 Nyiri Desert in Kenya; the 7000 km^2 Guban Desert in Somalia; the 81,000 km^2 Namib Desert in Angola, Namibia, and South Africa; the 100,000 km^2 Chalbi Desert in Kenya; the 136,956 km^2 Danakil Desert in Djibouti, Eritrea, and Ethiopia; the 400,000 km^2 Karoo Desert in South Africa; and the 930,000 km^2 Kalahari Desert in Botswana, Namibia, and parts of South Africa and Western Zimbabwe. Besides, this region is bordered by the 9.2 million km^2 Sahara Desert in the North (https://safarisafricana.com/deserts-in-africa/).

Of the limited studies that have been carried out in SSA to determine the stress alleviation potentials of extremophiles on crops, Enquahone et al. (2022) from Ethiopia report on the plant ability of some halotolerant bacterial strains to solubilise phosphate, fix nitrogen, as well as produce indole-3-acetic acid (IAA) and hydrogen cyanide, showing their potential ability to both promote plant growth as well as biocontrol plant pathogens (Akinola et al. 2021). These isolates also exhibited tolerance to abiotic stress by growing in high NaCl concentrations and under growth temperatures of up to 50 °C, showing their potential to foster plant tolerance to salinity and drought stress. These abilities were, however, not proof-tested on plants as they were not used to inoculate crops. Without this proof, the observed results remain inconclusive. Further north, Nafis et al. (2019) characterised some extremophilic actinobacteria for plant growth promoting traits in Morocco, with their findings showing that the actinobacteria, belonging to the genera *Streptomyces, Nocardioides, Saccharomonospora, Actinomadura*, and *Prauserella* could solubilise inorganic phosphate and potassium, fix nitrogen, as well as produce siderophores and IAA. While all these traits are characteristic of plant growth promoting microorganisms, the limitation with this particular study was also the failure to prove these traits using inoculation experiments, which could have been done under greenhouse settings. On the other hand, however, these results are a glimmer of the hope for climate adapted agriculture that lies with as yet unexploited potential of extremophiles in SSA, and Africa as a whole.

In Namibia, Southern Africa, Chimwamurombe et al. (2016) assessed the plant growth promoting traits of Marama bean seed associated bacterial endophytes. The plant grows in nutrient poor sandy soils that are frequently exposed to high light intensity, extreme temperatures, and

prolonged moisture stress, which places the endophytes into the category of extremophiles. Like the other studies already highlighted, the isolates turned out positive for plant growth promoting traits, including the production of IAA, siderophores, ACC deaminase, as well as the ability to solubilise phosphate and fix nitrogen. The limitation with this study, which the authors also alluded to, is that though the isolates proved positive for a myriad of plant growth promoting traits *in vitro*, they were not tested *in planta*, and so their plant growth promoting capabilities remain unproven.

Adeleke and Dames (2014) showed that bacteria associated with the Kalahari truffle (*Kalaharituber pfeilii*), known as mycorrhization helper bacteria (MHB) are capable of stimulating fungal growth and exhibiting plant growth-promoting activities. These bacterial isolates belonging to different phyla including Proteobacteria, Firmicutes, and Actinobacteria exhibited plant growth promoting traits such as IAA production, phosphate solubilization, and stimulation of mycelial growth *in vitro*, suggesting that they play a pivotal role in aiding fungal growth in desert conditions. Correspondingly, Cherif et al. (2015) discovered that some endophytic bacteria (under the phyla Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes) associated with the date palm (*Phoenix dactylifera* L.) roots exhibited tolerance to salt and drought stress, and variable tolerance to high temperatures. In a promising development for the production of extremophile based biofertilisers in Africa, some strains belonging to the genus *Pseudomonas* showed PGP activity *in planta* when, in experiments used to inoculate date palms, they significantly enhanced their growth under drought conditions. Besides extremophiles, mesophile bacteria with plant growth promoting traits have been shown to not only promote plant growth but to also increase yield. As a case in point, Amogou et al. (2019) showed that maize inoculated with a combination of *Serratia marcescens* and 50% chemical fertiliser (NPK fertiliser) in open field conditions resulted in significant increases in plant height, fresh root biomass, dry apical biomass, dry root biomass, and grain yield compared to uninoculated control plants though with a similar NPK treatment. Given that the vast majority of such studies are based on green-house experiments, the findings of this study confirm the viability of applying plant growth promoting microorganisms in open field conditions, with remarkable returns.

There is therefore room for expansion into assessing the plant growth promoting abilities of extremophiles in drought prone field conditions in this region as a way of ensuring food security in this era of global warming and climate change. However, there are still a number of hurdles which must be overcome for this to become a reality. One such limitation that seems to have confined biofertiliser researchers to greenhouses is the poor adaptability of bioinoculants to the different agro-ecosystems in which they are applied in order to be of any ecological and economic benefit (Zenteno-Alegría et al. 2024). There is need to build capacity in extremophile agricultural biotechnology in this region, primarily in the form of bioprospecting for isolates exhibiting aggressive plant growth promoting capabilities. That objective should concurrently be pursued with inoculum adaptation trials under open field situations and for such trials to be repeated over multiple growing seasons in which the bioinoculants are likely to be tested through exposure to different biotic and abiotic factors before they can be certified suitable for commercial distribution as biofertilisers. Priority should also be given to understanding the likely ecological effects of extremophile biofertiliser application into agroecosystems from which they did not originate, determining potential biosecurity issues, and ensuring equitable socioeconomic rewards. Moreover, improvements in the biotechnological components of extremophile use as biofertilisers, including standardisation protocols, scalability issues, and cost-effectiveness are required. Finally, effective collaboration among scientific communities, policymakers, and regulatory agencies is essential for creating strong frameworks that would regulate the utilisation of extremophiles in agriculture.

Conclusion

The food security situation in sub-Saharan Africa (SSA) is under threat owing to its above global average population growth *per capita*. Adding on to that is climate change which, in this region, manifests in recurrent droughts, above global average temperatures, and soil salinisation which are projected to further reduce agricultural productivity. The impacts of climate change on agricultural output in SSA are exacerbated by its already high baseline temperatures, as well as its lack of climate change mitigation measures. However, extremophiles are emerging as a likely solution to climate change induced food insecurity as they have been proven to not only promote plant growth, but to also foster plant tolerance to drought, heat and salinity stress by inducing a combination of molecular and physiological responses. However, compared to other regions, the SSA region is lagging behind in this research, despite being endowed with numerous extreme environments from which extremophiles with both plant growth and stress alleviation traits could potentially be isolated. Even in regions where extremophiles have been trialled for plant growth promotion and stress alleviation, these trials have largely been limited to greenhouse settings. There is still need to bridge the gap between research and practice by applying extremophile-based biofertilisers to crops in open field agro-ecosystems under natural conditions to holistically evaluate their effec-

tiveness in enhancing crop productivity under drought stress and hence meet the food demands of the SSA population. To achieve this, we recommend that research be done to achieve the following:

- expand the scope of extremophile-based biofertilisers research in SSA both in scale as well as in setting, by taking it beyond the greenhouse into the open field.
- carry out adaptability trials of extremophile-based biofertilisers in open field ecosystems to ascertain the extent to which they survive in agroecosystems, as well as how well they compete against native microbial populations.
- determine the impact of extremophile-based biofertilisers on both crop survival and yield enhancement under drought and salinity stress in open field conditions.

Acknowledgements BRH is grateful for funding of German-African Cooperation by the Federal Ministry of Education and Research (BMBF), grants SASSCAL2-Sustain (01LG2051A) and SusTec (01DG21008), and by the German Academic Exchange Service (DAAD, grant no. 57558109).

Author Contribution All authors contributed to the study conception and design. Data collection and analysis were performed by Timothy Sibanda, Ramganesh Selvarajan and Barbara Reinhold-Hurek. The first draft of the manuscript was written by Timothy Sibanda and all authors revised and commented on it. All authors read and approved the final manuscript.

Funding Open access funding provided by University of the Witwatersrand.

Data Availability No data was generated in this process of compiling this manuscript.

Conflict of interest T. Sibanda, R. Selvarajan and B. Reinhold-Hurek declare that they have no competing interests.

Open Access Dieser Artikel wird unter der Creative Commons Namensnennung 4.0 International Lizenz veröffentlicht, welche die Nutzung, Vervielfältigung, Bearbeitung, Verbreitung und Wiedergabe in jeglichem Medium und Format erlaubt, sofern Sie den/die ursprünglichen Autor(en) und die Quelle ordnungsgemäß nennen, einen Link zur Creative Commons Lizenz beifügen und angeben, ob Änderungen vorgenommen wurden. Die in diesem Artikel enthaltenen Bilder und sonstiges Drittmaterial unterliegen ebenfalls der genannten Creative Commons Lizenz, sofern sich aus der Abbildungslegende nichts anderes ergibt. Sofern das betreffende Material nicht unter der genannten Creative Commons Lizenz steht und die betreffende Handlung nicht nach gesetzlichen Vorschriften erlaubt ist, ist für die oben aufgeführten Weiterverwendungen des Materials die Einwilligung des jeweiligen Rechteinhabers einzuholen. Weitere Details zur Lizenz entnehmen Sie bitte der Lizenzinformation auf http://creativecommons.org/licenses/by/4.0/deed.de.

References

Adeleke R, Dames JF (2014) Kalaharituber pfeilii and associated bacterial interactions. South Afr J Bot 90:68–73. https://doi.org/10.1016/j.sajb.2013.10.003

Akinbode SO, Okuneye PA, Onyeukwu CO (2022) Inequality, population growth, and hunger in Sub-Saharan Africa. socscie. https://doi.org/10.1007/s43545-022-00554-x

Akinola SA, Ayangbenro AS, Babalola OO (2021) The diverse functional genes of maize rhizosphere microbiota assessed using shotgun metagenomics. J Sci Food Agric 101:3193–3201. https://doi.org/10.1002/jsfa.10948

Alori ET, Emmanuel OC, Glick BR, Babalola OO (2020) Plant–archaea relationships: a potential means to improve crop production in arid and semi-arid regions. World J Microbiol Biotechnol. https://doi.org/10.1007/s11274-020-02910-6

Alsharif W, Saad MM, Hirt H (2020) Desert microbes for boosting sustainable agriculture in extreme environments. Front Microbiol 11:1666. https://doi.org/10.3389/fmicb.2020.01666

Amjath-Babu TS, Krupnik TJ, Aravindakshan S et al (2016) Climate change and indicators of probable shifts in the consumption portfolios of dryland farmers in Sub-Saharan Africa: Implications for policy. Ecol Indic 67:830–838. https://doi.org/10.1016/j.ecolind.2016.03.030

Amogou O, Dagbénonbakin G, Agbodjato NA et al (2019) Applying rhizobacteria on maize cultivation in northern Benin: effect on growth and yield. AS 10:763–782. https://doi.org/10.4236/as.2019.106059

Andrés-Barrao C, Lafi FF, Alam I et al (2017) Complete genome sequence analysis of Enterobacter sp. SA187, a plant multistress tolerance promoting endophytic bacterium. Front Microbiol 8:2023. https://doi.org/10.3389/fmicb.2017.02023

Arumugam P, Chemura A, Aschenbrenner P et al (2023) Climate change impacts and adaptation strategies: an assessment on sorghum for Burkina Faso. Eur J Agron 142:1–26. https://doi.org/10.1016/j.eja.2022.126655

Ayangbenro AS, Babalola OO (2021) Reclamation of arid and semi-arid soils: the role of plant growth-promoting archaea and bacteria. Curr Plant Biol. https://doi.org/10.1016/j.cpb.2020.100173

Ayugi B, Eresanya EO, Onyango AO et al (2022) Review of meteorological drought in Africa: historical trends, impacts, mitigation measures, and prospects. Pure Appl Geophys 179:1365–1386. https://doi.org/10.1007/s00024-022-02988-z

Bang C, Dagan T, Deines P et al (2018) Metaorganisms in extreme environments: do microbes play a role in organismal adaptation? Zoology 127:1–19. https://doi.org/10.1016/j.zool.2018.02.004

ten Berge HFM, Hijbeek R, van Loon MP et al (2019) Maize crop nutrient input requirements for food security in sub-Saharan Africa. Glob Food Sec 23:9–21. https://doi.org/10.1016/j.gfs.2019.02.001

Bhaga TD, Dube T, Shekede MD, Shoko C (2020) Impacts of climate variability and drought on surface water resources in sub-Saharan Africa using remote sensing: a review. Remote Sens 12(24):4184. https://doi.org/10.3390/rs12244184

Bokhari A, Essack M, Lafi FF et al (2019) Bioprospecting desert plant Bacillus endophytic strains for their potential to enhance plant stress tolerance. Sci Rep 10:3001. https://doi.org/10.1038/s41598-020-58957-w

Cairns JE, Hellin J, Sonder K et al (2013) Adapting maize production to climate change in sub-Saharan Africa. Food Secur 5:345–360. https://doi.org/10.1007/s12571-013-0256-x

Cairns JE, Chamberlin J, Rutsaert P et al (2021) Challenges for sustainable maize production of smallholder farmers in sub-Saharan Africa. J Cereal Sci 101:1–8. https://doi.org/10.1016/j.jcs.2021.103274

Calzadilla A, Zhu T, Rehdanz K et al (2013) Economywide impacts of climate change on agriculture in sub-Saharan Africa. Ecol Econ 93:150–165. https://doi.org/10.1016/j.ecolecon.2013.05.006

de Carvalho MHC (2008) Drought stress and reactive oxygen species. Plant Signal Behav 3(3):156–165. https://doi.org/10.4161/psb.3.3.5536

Charrier A, Rippa S, Yu A et al (2012) The effect of carnitine on Arabidopsis development and recovery in salt stress conditions. Planta 235:123–135. https://doi.org/10.1007/s00425-011-1499-4

Chen C, Xin K, Liu H et al (2017) Pantoea alhagi, a novel endophytic bacterium with ability to improve growth and drought tolerance in wheat. Sci Rep 7:41564. https://doi.org/10.1038/srep41564

Chen L, Liu Y, Wu G et al (2016) Induced maize salt tolerance by rhizosphere inoculation of Bacillus amyloliquefaciens SQR9. Physiol Plant 158:34–44. https://doi.org/10.1111/ppl.12441

Cherif H, Marasco R, Rolli E et al (2015) Oasis desert farming selects environment-specific date palm root endophytic communities and cultivable bacteria that promote resistance to drought. Environ Microbiol Rep 7:668–678. https://doi.org/10.1111/1758-2229.12304

Chimwamurombe PM, Grönemeyer JL, Reinhold-Hurek B (2016) Isolation and characterization of culturable seed-associated bacterial endophytes from gnotobiotically grown Marama bean seedlings. FEMS Microbiol Ecol 92:1–11. https://doi.org/10.1093/femsec/fiw083

Chun SC, Paramasivan M, Chandrasekaran M (2018) Proline accumulation influenced by osmotic stress in arbuscular mycorrhizal symbiotic plants. Front Microbiol. https://doi.org/10.3389/fmicb.2018.02525

Di Falco S, Kis AB, Viarengo M, Das U (2024) Leaving home: cumulative climate shocks and migration in sub-Saharan Africa. Environ Resour Econ 87:321–345. https://doi.org/10.1007/s10640-023-00826-x

Dossa K, Miassi YE (2023) Exploring the nexus of climate variability, population dynamics, and maize production in Togo: implications for global warming and food security. Farming Syst 1:1–12. https://doi.org/10.1016/j.farsys.2023.100053

Eida AA, Ziegler M, Lafi FF et al (2018) Desert plant bacteria reveal host influence and beneficial plant growth properties. PLoS ONE 13:208223. https://doi.org/10.1371/journal.pone.0208223

Eida AA, Alzubaidy HS, de Zélicourt A et al (2019) Phylogenetically diverse endophytic bacteria from desert plants induce transcriptional changes of tissue-specific ion transporters and salinity stress in Arabidopsis thaliana. Plant Sci 280:228–240. https://doi.org/10.1016/j.plantsci.2018.12.002

Enquahone S, van Marle G, Simachew A (2022) Plant growth-promoting characteristics of halotolerant endophytic bacteria isolated from Sporobolus specatus (Vahr) Kunth and Cyperus laevigatus L. of Ethiopian rift valley lakes. Arch Microbiol. https://doi.org/10.1007/s00203-022-03021-6

Ezeh A, Kissling F, Singer P (2020) Why sub-Saharan Africa might exceed its projected population size by 2100. Lancet. https://doi.org/10.1016/S0140-6736(20)31522-1

Gbegbelegbe S, Chikoye D, Alene A et al (2023) Strategic foresight analysis of droughts in southern Africa and implications for food security. Front Sustain Food Syst 7:1159901. https://doi.org/10.3389/fsufs.2023.1159901

Gil T, Teixeira R, Sousa A et al (2023) Isolation and characterization of culturable osmotolerant microbiota in hypersaline and hypergypsic soils as new treatment for osmotic stress in plants. Soil Syst 7:7040086. https://doi.org/10.3390/soilsystems7040086

Gittard M (2023) Climate change, droughts, and water pollution in sub-Saharan Africa. E'cole des Ponts ParisTech

Gupta A, Mishra R, Rai S et al (2022) Mechanistic insights of plant growth promoting bacteria mediated drought and salt stress tolerance in plants for sustainable agriculture. Int J Mol Sci 23:23073741. https://doi.org/10.3390/ijms23073741

Hnini M, Aurag J (2024) Unlocking the diversity and plant-growth promoting potential of the bulk soil bacteria associated with the Saharan tree Vachellia tortilis subsp. raddiana. Soil Sci Soc Am J. https://doi.org/10.1002/saj2.20689

Hussain HA, Hussain S, Khaliq A et al (2018) Chilling and drought stresses in crop plants: Implications, cross talk, and potential management opportunities. Front Plant Sci 9:393. https://doi.org/10.3389/fpls.2018.00393

Inostroza NG, Barra PJ, Wick LY et al (2017) Effect of rhizobacterial consortia from undisturbed arid- and agro-ecosystems on wheat growth under different conditions. Lett Appl Microbiol 64:158–163. https://doi.org/10.1111/lam.12697

Joanna KO, Łukasz D, Ewelina R (2023) Proline concentrations in seedlings of woody plants change with drought stress duration and are mediated by seed characteristics: a meta-analysis. Sci Rep 13:15157. https://doi.org/10.1038/s41598-023-40694-5

Kaur G, Asthir B (2017) Molecular responses to drought stress in plants. Biol plant 61:201–209. https://doi.org/10.1007/s10535-016-0700-9

Kochhar N, Kavya IK, Shrivastava S et al (2022) Perspectives on the microorganism of extreme environments and their applications. Curr Res Microb Sci 3:1–16. https://doi.org/10.1016/j.crmicr.2022.100134

Kranner I, Beckett R, Hochman A, Nash TH (2008) Desiccation-tolerance in lichens: a review. Bryologist 111(4):576–593 (https://www.jstor.org/stable/20485752)

Lottering S, Mafongoya P, Lottering R (2021) Drought and its impacts on small-scale farmers in sub-Saharan Africa: a review. South Afr Geo J 103:319–341. https://doi.org/10.1080/03736245.2020.1795914

Marasco R, Rolli E, Vigani G et al (2013) Are drought-resistance promoting bacteria cross-compatible with different plant models? Plant Signal Behav 8:26741. https://doi.org/10.4161/psb.26741

Mekonen AA, Berlie AB, Ferede MB (2020) Spatial and temporal drought incidence analysis in the northeastern highlands of Ethiopia. Geoenviron Dis 7:10. https://doi.org/10.1186/s40677-020-0146-4

Mubeng-Tshitaka J-L, Muteba Mwamba JW, Dikgang J, Gelo D (2023) Risk spillover between climate variables and the agricultural commodity market in East Africa. Clim Risk Manag 42:1–21. https://doi.org/10.1016/j.crm.2023.100561

Mukhtar S, Mehnaz S, Malik KA (2019) Microbial diversity in the rhizosphere of plants growing under extreme environments and its impact on crop improvement. Environ Sustain 2:329–338. https://doi.org/10.1007/s42398-019-00061-5

Mukhtar S, Zareen M, Khaliq Z et al (2020) Phylogenetic analysis of halophyte-associated rhizobacteria and effect of halotolerant and halophilic phosphate-solubilizing biofertilizers on maize growth under salinity stress conditions. J Appl Microbiol 128:556–573. https://doi.org/10.1111/jam.14497

Munir N, Hanif M, Abideen Z et al (2022) Mechanisms and strategies of plant microbiome interactions to mitigate abiotic stresses. Agron 12:1–33. https://doi.org/10.3390/agronomy12092069

Nafis A, Raklami A, Bechtaoui N et al (2019) Actinobacteria from extreme niches in Morocco and their plant growth-promoting potentials. Divers (basel) 11:1–15. https://doi.org/10.3390/d11080139

Naik K, Mishra S, Srichandan H et al (2019) Plant growth promoting microbes: Potential link to sustainable agriculture and environment. Biocatal Agric Biotechnol 21:101326. https://doi.org/10.1016/j.bcab.2019.101326

Nath Yadav A (2017) Beneficial role of extremophilic microbes for plant health and soil fertility. J Agric Sci Bot 1(1):9–12. https://doi.org/10.35841/2591-7897.1.1.30-33

Ofori SA, Cobbina SJ, Obiri S (2021) Climate change, land, water, and food security: perspectives from sub-Saharan Africa. Front Sustain Food Syst 5:1–9. https://doi.org/10.3389/fsufs.2021.680924

Oney-Birol S (2019) Exogenous L-carnitine promotes plant growth and cell division by mitigating genotoxic damage of salt stress. Sci Rep 9(1):17229. https://doi.org/10.1038/s41598-019-53542-2

Osman JR, de Zelicourt A, Bisseling T et al (2016) Bacterial rhizosphere biodiversity from several pioneer desert sand plants near Jizan, Saudi Arabia. Open Conf Proc J 7:70–79. https://doi.org/10.2174/2210289201607020070

Palacio-Rodríguez R, Coria-Arellano JL, López-Bucio J et al (2017) Halophilic rhizobacteria from Distichlis spicata promote growth and improve salt tolerance in heterologous plant hosts. Symbiosis 73:179–189. https://doi.org/10.1007/s13199-017-0481-8

Parida A, George S (2015) Sustaining and enhancing crop productivity in an era of climate change. Curr Sci 109:462–473 (https://www.jstor.org/stable/24906101)

Phillips K, Ludidi N (2017) Drought and exogenous abscisic acid alter hydrogen peroxide accumulation and differentially regulate the expression of two maize RD22-like genes. Sci Rep 7:8821. https://doi.org/10.1038/s41598-017-08976-x

Pondi EM, Choi M, Mitra P (2022) Sub-Saharan Africa: Building resilience to climate-related disasters, WP/22/39, February 2022. https://www.imf.org/en/Publications/WP/Issues/2022/02/25/Sub-Saharan-Africa-Building-Resilience-to-Climate-Related-Disasters-513578. Accessed 26 June 2024

Raklami A, Babalola OO, Jemo M, Nafis A (2024) Unlocking the plant growth-promoting potential of yeast spp.: Exploring species from the Moroccan extremophilic environment for enhanced plant growth and sustainable farming. FEMS Microbiol Lett. https://doi.org/10.1093/femsle/fnae015

Rani S, Kumar P, Suneja P (2021) Biotechnological interventions for inducing abiotic stress tolerance in crops. Plant Gene 27:100315. https://doi.org/10.1016/j.plgene.2021.100315

Salahuddin M, Gow J, Vink N (2020) Effects of environmental quality on agricultural productivity in sub-Saharan African countries: a second generation panel based empirical assessment. Sci Total Environ 741:1–10. https://doi.org/10.1016/j.scitotenv.2020.140520

Sangeetha J, Prathima P, Thangadurai D et al (2016) Chapter 1: Exploring microbes from extreme environments for crop productivity and environmental sustainability. In: Bagyaraj DJ, Jamaluddin (eds) Microbes for Plant Stress Management. New India Publishing Agency, New Delhi, pp 1–24

Santos LF, Olivares FL (2021) Plant microbiome structure and benefits for sustainable agriculture. Curr Plant Biol 26:100198. https://doi.org/10.1016/j.cpb.2021.100198

Santos AP, Belfiore C, Úrbez C et al (2023) Extremophiles as plant probiotics to promote germination and alleviate salt stress in soybean. J Plant Growth Regul 42:946–959. https://doi.org/10.1007/s00344-022-10605-5

Santpoort R (2020) The drivers of maize area expansion in sub-Saharan Africa. How policies to boost maize production overlook the interests of smallholder farmers. Land 9:1–13. https://doi.org/10.3390/land9030068

Selim S, Hassan YM, Saleh AM et al (2019) Actinobacterium isolated from a semi-arid environment improves the drought tolerance in maize (Zea mays L.). Plant Phys Biochem 142:15–21. https://doi.org/10.1016/j.plaphy.2019.06.029

Serdeczny O, Adams S, Baarsch F et al (2017) Climate change impacts in sub-Saharan Africa: from physical changes to their social repercussions. Reg Environ Change 17:1585–1600. https://doi.org/10.1007/s10113-015-0910-2

Shukla S, Husak G, Turner W et al (2021) A slow rainy season onset is a reliable harbinger of drought in most food insecure regions in sub-Saharan Africa. PLoS ONE 16:242883. https://doi.org/10.1371/journal.pone.0242883

Singh RP, Jha PN (2016) The multifarious PGPR Serratia marcescens CDP-13 augments induced systemic resistance and enhanced salinity tolerance of wheat (Triticum aestivum L.). PLoS ONE 11:155026. https://doi.org/10.1371/journal.pone.0155026

Stuch B, Alcamo J, Schaldach R (2020) Projected climate change impacts on mean and year-to-year variability of yield of key smallholder crops in sub-Saharan Africa. Clim Dev. https://doi.org/10.1080/17565529.2020.1760771

Tadesse T, Senay GI, Wardlow BD et al (2008) The need for integration of drought monitoring tools for proactive food security management in sub-Saharan Africa. Nat Resour Forum 32:265–279. https://doi.org/10.1111/j.1477-8947.2008.00211.x

Takahashi F, Kuromori T, Urano K et al (2020) Drought stress responses and resistance in plants: from cellular responses to long-distance intercellular communication. Front Plant Sci 11:1–14. https://doi.org/10.3389/fpls.2020.556972

Torbaghan ME, Hossein G, Torghabe K (2023) Evaluation of three groups of plant growth-promoting extremophilic rhizospheric bacteria on induction of salinity and alkalinity tolerance in GN15 almond (Prunus amygdalus L.) rootstocks. J Plant Process Funct 12(55):1–14 (http://jispp.iut.ac.ir/article-1-1838-fa.html)

Tuesta-Popolizio DA, Velázquez-Fernández JB, Rodriguez-Campos J, Contreras-Ramos SM (2021) Isolation and identification of extremophilic bacteria with potential as plant growth promoters (Pgpb) of a geothermal site: a case study. Geomicrobiol J 38:436–450. https://doi.org/10.1080/01490451.2021.1879972

Uzilday RO, Ganie SA (2023) Editorial: Extremophiles: tolerance mechanisms and use in crop improvement. Front Plant Sci 14:1233202. https://doi.org/10.3389/fpls.2023.1233202

Waha K, Müller C, Bondeau A et al (2013) Adaptation to climate change through the choice of cropping system and sowing date in sub-Saharan Africa. Glob Environ Chang 23(1):130–143. https://doi.org/10.1016/j.gloenvcha.2012.11.001

Warsame AA, Sheik-Ali IA, Jama OM et al (2022) Assessing the effects of climate change and political instability on sorghum production: empirical evidence from Somalia. J Clean Prod 360:1–9. https://doi.org/10.1016/j.jclepro.2022.131893

Wilhite DA, Glantz MH, And Glantz MH (1985) Understanding the drought phenomenon: the role of definitions. Water Int 10:111–120. https://doi.org/10.1080/02508068508686328

Xie F, Pathom-aree W (2021) Actinobacteria from desert: diversity and biotechnological applications. Front Microbiol 12:1–27. https://doi.org/10.3389/fmicb.2021.765531

Xu SY, Weng J (2020) Climate change shapes the future evolution of plant metabolism. Adv Gen 1:10022. https://doi.org/10.1002/ggn2.10022

Yadav AN (2021) Biodiversity and bioprospecting of extremophilic microbiomes for agro-environmental sustainability. J Appl Biol Biotechnol 9:1–6. https://doi.org/10.7324/JABB.2021.9301

Zenteno-Alegría CO, Yarzábal Rodríguez LA, Ciancas Jiménez J et al (2024) Fungi beyond limits: The agricultural promise of extremophiles. Microb Biotechnol 17(3):e14439. https://doi.org/10.1111/1751-7915.14439

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.