Plant Growth Regulation (2023) 100:7–24
https://doi.org/10.1007/s10725-022-00951-5

REVIEW

Plant growth promoting microorganisms mediated abiotic stress tolerance in crop plants: a critical appraisal

Nadia Gul[1] · Ishfaq Ahmad Wani[2] · Rakeeb Ahmad Mir[3] · Javaid Ashraf Nowshehri[4] · Shabana Aslam[5] · Renu Gupta[6] · Susheel Verma[7] · Saima Aslam[1]

Received: 14 July 2022 / Accepted: 15 December 2022 / Published online: 3 January 2023

Abstract
Under the constant strain of rising environmental changes it is now more important than ever to describe and understand plant microbe interactions in terms of abiotic stress resistance. Multi omics including transcriptomics, genomics, RNomics etc. like approaches bring together studies on plants interactions with microbes and plant growth regulators to provide multi layered data. Comprehensive understanding of plant microbe mediated mechanisms and hormone signaling networks for abiotic stress tolerance is necessary to translate their practical use for plant survival under extreme conditions. This will pave the way for climate smart agriculture research that will help in progress and manipulation of advantageous microbes and plant regulators as foundation of crop acclimation to changing climatic conditions thereby strengthening further sustainable agriculture. For crop development, it is crucial to understand the fine tuning and integration of many signals created by microbial interactions in plants. This study discusses plant responses to microbe mediated stress relief that have been documented so far. Analyzing the plant characteristics that were heterogeneously related to soil metabolites, minerals, and microorganisms utilizing omics techniques. This will aid in the further adoption of omics-based methodologies while taking into account the various tactics used by microorganisms. Present review provides indepth understanding of the interplay between Plant growth promoting microorganisms with crop plants to circumvent the undesirable impacts of environmental stress on crop cultivar and will help to implement omics based strategies to overcome abiotic stresses in plants.

Keywords Plant growth promoting microorganisms (PGPM) · Abiotic stress · Bioactive compounds · Sustainable agricultural growth

Introduction

Extreme climatic events tend to cause the global crop damage due to increased frequency of climatic change (Fedoroff et al. 2010). The goal of achieving global food security will be severely hampered by these changing environmental patterns, which could pose serious threats to the crops (Porfirio et al. 2018; Ali et al. 2022). Most abiotic stresses that affect plant machinery includes drought, flooding, extreme temperature, salinity and nutrient deficiency. These abiotic stresses tend to hinder plant development, growth and productivity (Bailey-Serres and Voesenek 2008; Khan et al. 2019). The

Communicated by Hang-Wei Hu.

✉ Saima Aslam
saima@bgsbu.ac.in

[1] Department of Biotechnology, School of Biosciences and Biotechnology, Baba Ghulam Shah Badshah University, Rajouri 185234, India

[2] Department of Botany, Baba Ghulam Shah Badshah University, Rajouri 185234, India

[3] Department of Biotechnology, School of Life Sciences, Central University of Kashmir, Ganderbal, Jammu & Kashmir, India

[4] Department of Pharmaceutical Sciences, University of Kashmir, Srinagar 190006, India

[5] Department of Botany, Sri Pratap College, Srinagar 190001, India

[6] Division of Soil Science and Agricultural Chemistry, Faculty of Agriculture, Sher-e- Kashmir University of Agricultural Sciences and Technology, Chatha, Jammu 180009, India

[7] Department of Botany, University of Jammu, Jammu 180001, India

extremity of abiotic stress response depends on exposure of particular stressor or in combination, duration of exposure, growing stage and the susceptible of plant cultivar (Sorty et al. 2018). Stress alleviating approaches to the adverse nature of abiotic stresses are important global agriculture drivers to optimize the crop productivity under detrimental environmental conditions (Nutan et al. 2020). Execution of different intrinsic combating mechanisms tend to cease the negative consequences of abiotic stressors which includes accumulation of osmolytes, antioxidant enzyme expression, heat shock proteins etc. (Scarpeci et al. 2008; Prasch and Sonnewald 2013; Kumawat et al. 2022; Singh et al. 2022b). Microbes can help plants to cope with abiotic challenges by modifying their physiology (De Zelicourt et al. 2013; Maheshwari et al. 2021; Chandwani and Amaresan 2022). Under abiotic circumstances plant growth promoting microorganisms (PGPM) act as potent candidates to actively increase the level of antioxidants enzymes, osmolytes and stress based expression of genes (Hayat et al. 2010; Wang et al. 2012; Farrar et al. 2014; Notununu et al. 2022). So, these PGPMs have biochemical, molecular as well as physiological based response against stressor in plants imparting integral function of plant surveillance mechanisms and immunity (Hacquard et al. 2017). PGPM includes plant growth promoting bacteria/rhizobacteria (PGPR), plant growth stimulating fungi, actinomyctes, and bacteria involved in nitrogen fixing (Wani et al. 2015; Hassen et al. 2016; Elhindi et al. 2017; Jiménez-Mejía et al. 2022). These PGPM provides improved progression of crops and imparts tolerance against numerous environmental stresses (Bano and Fatima 2009; Lugtenberg and Kamilova 2009). Plant growth promoting bacteria (PGPB) induces the plant immune response so as to resist various infections (van Hulten et al. 2006). Moreover, these plant linked microbes support development of crops by synthesizing secondary metabolites, phytochemicals and hormone production (Mendes et al. 2011; Hardoim et al. 2015; Egamberdieva et al. 2017; Srinivasa et al. 2022). A deeper understanding regarding the interaction of microbes with plants under changing climatic conditions as well as the approaches employed by them to combat the negative effects of stress will ease out to predict the impact of climate change on primary productivity. This will also help to develop management and policy tools to increase the resilience of plant systems (Trivedi et al. 2022). A systems-based approach that takes into account the ecology of microbial communities may aid in improving the reliability of existing technologies while encouraging innovation and wider implementation (Jurburg et al. 2022). In current review, we thoroughly explored the impact of microorganisms in enhancing stress tolerance to a wide variety of abiotic stress factors for growth and development attributes plant. A special emphasis was put on enlisting the role of plant growth promoting microbes in activating antioxidant enzymes systems, sequestration of metal ions and combating the nutritional deficiencies. Moreover, we have detailed the mechanism of stress tolerance aided by plant growth promoting microbes through the production of siderophores, by several physiological adaptations, production of volatile organic substances (VOCs) and maintaining the higher K^+/Na^+ ratio.

Plant metabolite insights related to abiotic stress tolerance

The deeper knowledge of the many tolerance approaches for preserving agricultural yield through management of environmental variables might be beneficial in ensuring that crops retain their optimum genetic potential (Brooker et al. 2022). Phytohormones are plant growth factors that are produced in specific organs and have a significant influence on plant metabolism (Singh et al. 2022a). They also aid in the mitigation of abiotic stressors. Auxins are key phytohormones, and the auxin indole-3-acetic acid (IAA) has been found to induce cell division, elongation, and differentiation, among other growth and developmental processes along with mediating abiotic stress tolerance. Cytokinins (CK), a class of plant hormones, are involved in sustaining cellular proliferation and differentiation as well as preventing senescence, which results in the avoidance of early leaf senescence (Tariq and Ahmed 2022). Overexpression of genes involved in cytokinin production has been confirmed, as has their significance in stress tolerance. Under abiotic stress, ABA-induced and -mediated signaling regulates the expression of stress-responsive genes, resulting in greater elicitation of tolerance responses (Sah et al. 2016). Plant growth and development were discovered to be stimulated by gibberellic acid under a variety of abiotic stress situations (Waadt et al. 2022). Gibberellic acid promotes effective absorption and ion allocation in plants, resulting in increased growth and the maintenance of plant metabolism under normal and stressful conditions (Sherin et al. 2022). Through stress-activated signal pathways and response mechanisms, phytohormones affects various physiological processes involved in plant stress tolerance.

Plants have evolved a variety of defences at the phytochemical, biochemical, morphological, and molecular levels to deal with a wide range of environmental challenges. The buildup of numerous osmoprotectants such as polyamines (PAs), proline, glycine betaine (GB), and sugars is one of the key adaptive stress responses for improving stress in plants (Ramazan et al. 2022). All of these solutes contribute to the maintenance of homeostasis, the maintenance of cell turgor and water uptake, the scavenging of excess reactive oxygen species (ROS), and the re-establishment of cellular redox balance, all of which protect the cellular machinery from oxidative damage and osmotic stress (Ghosh et al. 2019).

PAs are small polycations that are involved in growth, and development and are well documented for their anti-senescence and anti-stress characteristics due to their acid balancing and antioxidant properties (Choudhary et al. 2022). PAs have been suggested to have a role in modifying plant defense responses to a variety of environmental stresses, such as salinity, oxidative stress, drought, chilling stress and metal toxicity (Sinha and Mishra 2022). GB is an essential osmolyte that helps plants grow and function properly. Plant species, on the other hand, differ in their ability to naturally accumulate GB. Plants accumulate diverse proportions of GB; GB accumulators naturally accumulate GB under normal and stress conditions (Ayub et al. 2022). Proline also appears to be promising in genetics and genomics techniques for improving plant adaptation responses to changing climatic circumstances (Ghosh et al. 2022).

Microbe facilitated abiotic stress tolerance mechanisms adopted by plants

Wide range of stress tolerance mechanism are adopted by plants in abiotic stress conditions depending upon the microbial variability and diversity (Elhindi et al. 2017; Van Oosten et al. 2017). Plant root rhizosphere is usually a site rich in nutrients such as, sugars, amino acids, fatty acids and secondary metabolites to act as strong chemoattractant for microbes. These microbes utilize plant metabolites to flourish in rhizosphere and in turn synthesize important biological chemicals, such as, compatible solutes, antifungal compounds, enzymes, gibberellins, cytokinins, auxins, and ABA (Figure 1). PGPM enhance growth and metabolism of crop through induction of wide range of metabolites such as, phytohormones synthesis, growth inducing metabolites, osmoprotectants, heavy metal sequestration, induction of siderophores, morpho-anatomic changes, modulating physiological attributes through induction of volatile compounds and positive modulation of nutrient profile (Kazan 2013). Positive modulations through PGPM to regulate plant

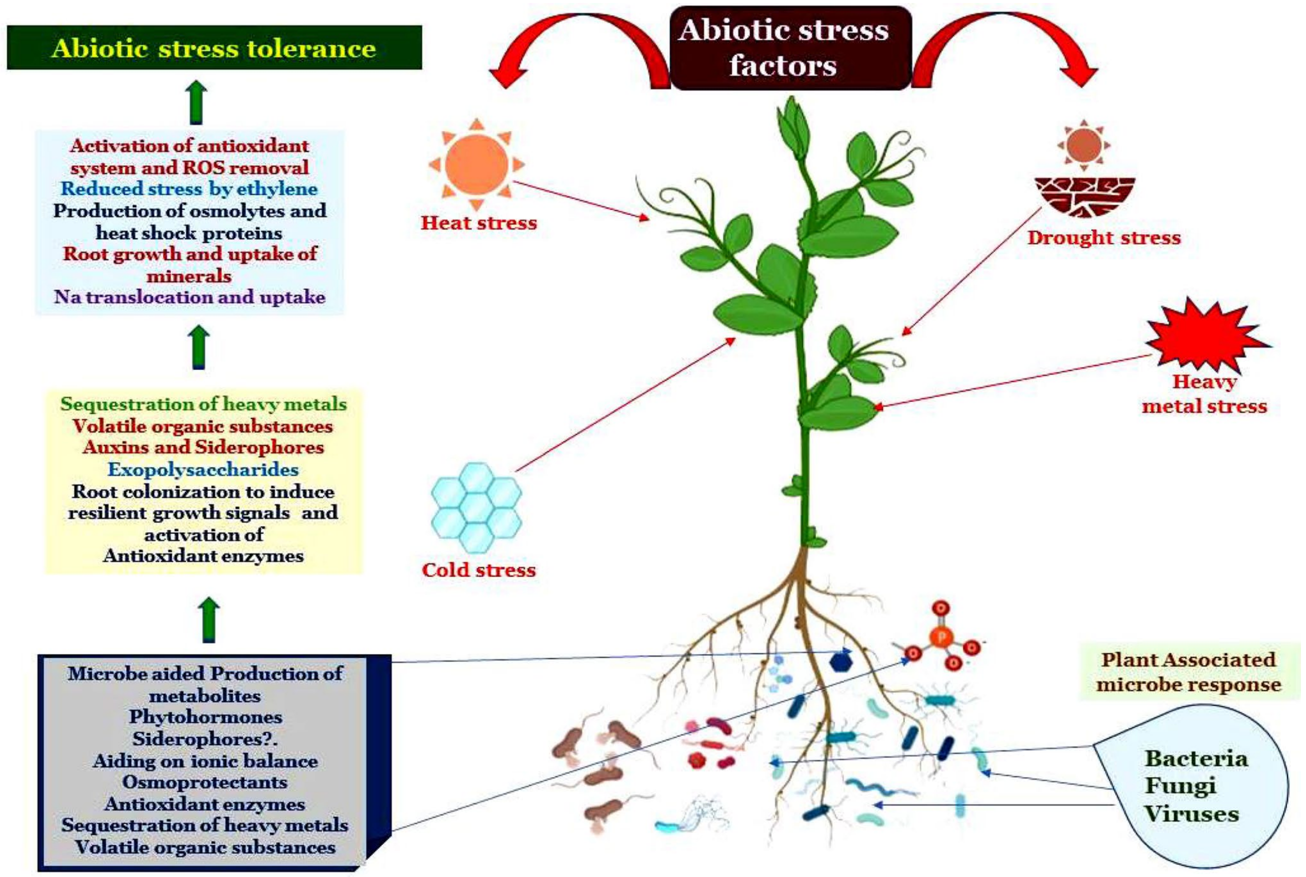

Fig. 1 Plant Growth Promoting Microorganisms mediated tolerance mechanisms adopted by crop plants to combat abiotic stresses. Microorganisms thrive in the rhizosphere by consuming plant metabolites and produce vital biological substances such suitable solutes, antifungal compounds, enzymes, gibberllins, cytokinins, auxins, and ABA

growth and metabolism are further discussed in the proceeding sections of this review.

Microbe derived plant growth hormone production

Plant development and metabolism are controlled by plant hormones including auxin, cytokinin, gibberellins, JA, abscisic acids and ethylene (Kazan 2013; da Silva et al. 2022). In addition, they are central elements in the fight against environment based stress in plants (Hu et al. 2013). Growth of plant is altered by abiotic stress via altered phytohormones production (Khan et al. 2014; Sati et al. 2022). However, the root associated microbes tend to promote the biosynthesis of metabolically active substances and regulators of growth in plants (Kudoyarova et al. 2014; Pereira et al. 2016; Asaf et al. 2017). The microbial metabolites modulate the growth of plants through induction of hormones almost prototypical to the application of exogenous hormonal treatments (Shahzad et al. 2016). Root associated bacteria like *Sinorhizobium* sp., *Marinobacterium* sp., *Rhizobium* sp., *Pseudomonas* sp., have remarkable role in indole-3-acetic-acid (IAA) production (Hayat et al. 2010). This bacterial IAA results in activation of 1-aminocyclopropane-1- carboxylate (ACC) deaminase that mediates degradation of ACC that acts as initiator molecule for ethylene synthesis (Glick 2005). In a study on the relationship between Trichoderma and plants, it was found that genotypic traits of plants can influence the way microbes and plants interact, which in turn affects plant growth and reduces stress. Degradation of IAA in the rhizosphere and ACC deaminase activity on tomato show the growth-promoting and stress-relieving activities of *T. atroviride* (Gravel et al., 2007). Through RNA interference, a potential ACC-deaminase sequence discovered in the Trichoderma genome was identified (Viterbo et al., 2010; Kubicek et al., 2011). Two types of ACC-deaminase genes (acdS) comparable to those of *Pseudomonas fluorescens* for reducing stress were discovered using PCR analysis in a study on potato endophytes. The whole *acdS* operon from an uncultivated endophyte was identified by analysis of clones found in metagenomic libraries, and the transcriptional regulator gene *acdR* was found to be located upstream of *acdS*. *Burkholderia*, a major member of the genus, included this operon (Nikolic et al., 2011). Induction of stress response genes was discovered in *Sinorhizobium meliloti* by next-generation RNA sequencing in IAA overproducing strains (Defez et al., 2016). In addition, it is reported that overall growth and improvement of plant under stressful conditions is promoted via decreased ethylene formation and relieving the ethylene based repression on synthesis of auxin based response factor (Kang et al., 2010). Several physiological parameters involving cell differentiation, seed germination, root elongation and photosynthesis etc. are influenced by the auxin homeostasis (Ahemad and Kibret 2014; Khedr et al. 2022; Mousavi et al. 2022; Rolón-Cárdenas et al. 2022) .

Root associated PGPR have remarkable role in inducing the synthesis of auxin to mediate plant growth and development. These auxin producing microbes include *Rhizobium* sp., *Psuedomonas* sp. etc., which are colonized positively by auxin (Suzuki et al. 2003; Chang et al. 2014; Cai et al. 2022; Mathur et al. 2022). Cytokinin is another phytohormone synthesized under the influence of microbes such as, *Bacillus, Azospirillum* and *Arthobacter*s (Gray and Smith 2005; Naz et al. 2009). While *Arthrobacter koreensis* produces auxin, gibberellic acid (GA), abssisic acid (ABA) and jasmonates (JA) (Piccoli et al. 2011). GA is produced in plants by *Aspergillus fumigatus* and *Azospirillum lipoferum* against abiotic stress (Creus et al. 2004; Khan et al. 2011). Endophytic *Phoma glomerata* fungi also produces GA, improves plants abiotic stress resilience (Waqas et al. 2012). Fungal inoculations tend to decrease the levels of ABA, but modifying levels of salicylic acid (SA) and JA that act as vital plant defense hormones under stress conditions (Shinozaki and Yamaguchi-Shinozaki 2007). *Psuedomonas putida* helps *Arabidopsis thaliana* to combat water stress by enhancing the endogenous levels of hormones involving GA, auxin, cytokinin and ABA (Ghosh et al. 2019). In addition this strain helps soyabean plants to ameliorate the drought and salt stress by enhancing GA production *Sphingomonas sp.* and *Paecilomyces formosus* provides combating ways against metal stress in soyabean plants via increased production of endogenous hormone concentrations including IAA, JA and GB (Bilal et al. 2018). So, microorganisms have a tendency for building up plant hormones, which enhance plant development and confer tolerance to abiotic stimuli, reducing abiotic stress in plants (Liu et al. 2013; Latef et al. 2016; Tiwari et al. 2020; Iqbal et al. 2022; Shah et al. 2022).

Plant growth inducing metabolites

The differential metabolic regulations of prime and secondary plant metabolites occurs in responses to abiotic stresses. Plant primary metabolites like carbohydrates and amino acids are fundamental requirements for plant growth and overall development. While other metabolites of secondary fate like flavonoids and alkaloids are consumed for plant protection and some allied functions depending on plant species (Akula and Ravishankar 2011; Yadav et al. 2021). PGPR has been seen to have capability of promoting productivity and growth of plants by metabolic modulation (Lugtenberg and Kamilova 2009). Metabolic and proteomic studies of crop plants under stress have shown differential protein expression and metabolite expression as that of non-stressed plants (Meena et al. 2017; Dissanayake et al. 2022; Patel et al. 2022; Wang et al. 2022). Differential metabolite accumulation of L-proline, L-glutamine, γ-aminobutyric acid

(GABA) succinic acid, uridine −5-diphosphate, pyruvic acid ascorbic acid, citric acid, glutathione etc. was reported by *Bacillus velezensis* treatment under different abiotic stress circumstances (Abd El-Daim et al. 2019). GABA is involved in the metabolism of amino acids, carbohydrates as well as the carbon-nitrogen balance and plant growth control (Shelp et al. 2017). Some plant-associated bacteria have a role in purine and pyrimidine metabolism, which might affect the quantity of plant metabolites (Izaguirre-Mayoral et al. 2018). The composition of plant phenolic compounds has been acknowledged to be affected by *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Azospirillum spp.* (Walker et al. 2011). The accumulation of monoterpenes such as, sabine hydrate, thymol, -terpinene and carvacrol took place in shoots of oregano roots with the inoculation of *Azospirillum brasilense* and *Pseudomonas fluorescens* (Banchio et al. 2010). *Rhizophagus irregularis* inoculation increased phosphorus levels and showed changes in the leaf metabolome in plants belonging to the Poaceae, Plantaginaceae and Fabaceae families (Schweiger et al. 2014). Moreover, as per recent reports endophytes augmentation can promote the medicinal plant species in storing potentially important secondary metabolites even under different abiotic stress conditions (Ogbe et al. 2020; Elnahal et al. 2022).

Osmoprotectants

Abiotic stress induced circumstances cause the modification of cellular functions of plant that involves the formation and buildup of osmolytes (Wang et al. 2018; Riaz et al. 2019; Hossain et al. 2022). The osmolytes have pivotal protective role in plants at cellular level against any damage. These osmolytes prevent protein denaturation thereby maintaining cellular integrity of plant without interfering with the normal physiology (Nahar et al. 2016). Depending upon chemical composition, osmolytes are divided into three types that includes amino acids, sugars (reducing and non-reducing) and betaines (Slama et al. 2015). According to study, plant osmolyte content and concentration vary depending on species and environmental stress (Lugan et al. 2010). Differential osmolyte concentration has been reported to be enhanced in crop plants upon inoculation by different strains of PGPR under abiotic stress environments. A plant growth-promoting rhizobacterium was inoculated into *Vitis vinifera.* At a low temperature, *Burkholderia phytofirmans* boosted grapevine physiological activity along with growth (Barka et al. 2006). The concentration of glycine betaine-based quaternary entities was greater in plants infected with *Pseudomonas pseudoalcaligenes* (Jha et al. 2011). Furthermore, in drought stress, seed priming of maize with bacteria *Pseudomonas* spp. strains resulted in greater amounts of carbohydrates, proline, and free amino acids (Vardharajula et al. 2011; Ibrahim and El-Sawah 2022). Report based on Trichoderma-plant interaction, established the effects of genotypic features of plants on the modification of microbe plant interaction (*Trichoderma atroviride* and *Trichoderma harzianum*) and ectoine for salt tolerance in *Halomonas elongata* OUT30018. Some of its genes involved in ectoine synthesis were cloned and inserted into the tobacco plant *Nicotiana tabacum* L. cv Bright Yellow 2 (BY2), which grew normally under these conditions and boosted resistance to osmotic shock by accumulating ectoine (Lucena and Wang 2022). As per several studies PGPM have vital function in imparting resistance against abiotic stressors through increased osmolyte and other metabolite accumulation. The desirable characteristic of *Miscanthus* grass that frequently differs among cultivars is chilling tolerance. Variation among its cultivars for chilling tolerance exists and is confirmed by the molecular expression of relevant genes for the accumulation of carbohydrates. The molecular marker of sensitive genes, expressed in sensitive genotypes, can be used to predict the loss of tolerance among variety (Purdy et al. 2013).

Antioxidant enzymes

Abiotic stress causes a significant rise in reactive oxygen species (ROS) that causes oxidative damage (Mittler 2002). There is need to equilibrate the ROS production to maintain growth of plant and physiology (Noctor et al. 2018). Under constant abiotic stress, the growth of plants is highly effected until complete halt of metabolism, leading to complete death. One strategy to lessen oxidative stress in plants is to supplement them with beneficial microbes that have a tendency to produce high amounts of antioxidant enzymes that can help diminish oxidative stress. The PGPM inoculants boosts antioxidant levels and minimizes ROS and oxidative stress that makes plant more resilient to abiotic challenges. The cellular homeostasis is disturbed by changes in water availability, pH, temperature, heavy metals and UV-B radiation. This results in increase in ROS like hydroxyl radical, superoxide anion, singlet oxygen and hydrogen peroxide (Khoshru et al. 2020). Microbial inoculants protect the plants from cellular damage imparted by ROS by increasing the production of antioxidants such superoxide dismutase (SOD), catalase (CAT), glutathione (GSH), ascorbate peroxidase (AsA), tocopherols and carotenoids (Arora et al. 2020; Lopes et al. 2021). Bacterial inoculants increase the antioxidant propensity of drought-stressed plants. Leaves of *Lactuca sativa L.* (Lettuce) were given *Pseudomonas mendocina Palleroni*, and *Glomus mosseae* or *Glomus intraradices* or alone. *P. mendocina* inoculated cultivars growing under extreme stress showed the highest levels of CAT activity. Under intermediate drought circumstances, fungal and bacterial inoculation increased total CAT and peroxidase activity. It is reported in the lettuce study, these beneficial microorganisms can be employed to eradicate plant oxidative stress (Kohler et al. 2008). The *Proteobacterium Xanthomonas citri*, on the other hand, has increased production of catalase (KatG), allowing to battle the task of oxidative burst by citrus plants during leaf infection. (Tondo et al. 2016). The SOD and CAT were increased but the H_2O_2 and lipid peroxidation levels diminished in the nodules of plants co-inoculated with *Bradyrhizobium* and *Paenibacillus graminis* or Actinomandura (Santos et al. 2018). Under saline stress plants inoculated with *Pseudomonas mendocina* showed very less oxidative damage (drying, necrosis and reduced chlorosis) related with non- inoculated salt-stressed plants. These effects were evident because of improved antioxidant enzyme activity (Bianco and Defez 2009). According to Koussevitzky et al. (2008), the cytosolic ascorbate peroxidase 1 gene Apx1 is especially needed for *Arabidopsis* to be tolerant of drought and heat stress. Also different antioxidant enzymes, including CAT, SOD, GR and peroxidase (POD), are produced by arbuscular mycorrhizal fungus (AMF) species to help reduce the impact of ROS produced under salinity stress (Kumar et al. 2022).

Biocontrol

Combination of different inoculant mixtures that are having synergetic approach of interaction, tend to improve the functioning of beneficial microbes. Different bacterial strains like *Bacillus, Rhizobium* and *Psuedomonas* improved plant development and growth as compared to single inoculant (Figueiredo et al. 2010). *Rhizobium- Azospirillum* combination was capable to rise the expression of nod genes. It also led to formation of nodulation factors in *Rhizobium etli* and *Rhizobium tropici* under absence or presence of 50mM saline conditions (Dardanelli et al. 2008). Moreover, co-inoculation of *Rhizobium* with *Bacillus megaterium* or *Pseudomonas striata* led to gain in crop yield, dry matter, and phosphorus assimilation considerably over the non-inoculated in legume plants (Elkoca et al. 2010). These also enhanced the tolerance level of plants to drought, salt by implementing stress adaptive mechanisms (Marulanda et al. 2010; Zhou et al. 2016; Seleiman et al. 2021; Kaur et al. 2022).

Combating nutrient deficiency

Plants that experience abiotic stresses are resilient on their capability to avoid or tolerate adverse abiotic stresses by developing adaptive mechanisms of productivity and survival. The mineral and nutritional status of plants are greatly affected due lack sufficient water status as seen in drought, saline kind of stresses due to which nutrients become unavailable to plant. This seems to cause further intensification of adversity due to prevailing stressful condition thereby eventually leading to decrease in crop productivity (Munns and Tester 2008). However, it is reported that soil microorganisms have a crucial part in the management of nutrients (Adhya et al. 2015). Nitrogen fixation has pivotal function in augmenting soil fertility, nitrogen-fixing bacteria aids the atmospheric nitrogen conversion for the plant to synthesize amino acids (Lata et al. 2018). Solubilization of phosphate is also an important aspect of plant. Microorganisms involved in Phosphorus solubilizing (PSMs) have an essential role in its mineralization and solubilization of phosphorus. The PSM's are largely composed of bacteria, fungi and serve as substitutes to fulfil the phosphate demands of plants (Mokrani et al. 2020). Among bacteria *Pseudomonas*, *Rhizobium* and *Bacillus*, while in fungi *Penicillium* and *Aspergillus* are most efficient phosphate solubilizers (Sharma et al. 2013). In addition, some microorganisms such as, *Pseudomonas sp., Azotobacter sp., Bacillus mucilaginosus, Klebsiella sp., Rhizobium sp.* and *Paenibacillus sp.*, play a very fundamental role in potassium solubilization in plants that also accounts its place among the most important minerals for overall functioning and development of plant (Liu et al. 2012; Mazahar and Umar 2022; Rawat et al. 2022).

Sequestration of heavy metals

Metal contamination is one among the different pollutions that prevail worldwide in water, soils, and air. Anthropogenic sources like mining, industries, waste disposal, metal smelting, corrosion of metals in use etc. are the main causes of metal pollution (Ahemad 2012). The release of metallic sewage have harmful effect on plant and animal health (Ma et al. 2016). Heavy metals disrupt the homeostasis and nutritional metabolism of plants and it is pertinent to investigate their accumulation and effect for assuring safety and sustainability of environment (Glick 2010; Asati et al. 2016). Bioremediation is a new technology for removing heavy metal pollution from soil that relies on plant associated bacteria (Ojuederie and Babalola 2017). Microbes have a higher level of complexity than other living species, and they can serve as a reliable indication of heavy metal stress (Praveen Kumar et al. 2014). The plant endophytes aid their host to tolerate heavy metals and reduce metal toxicity, particularly the root-associated endophytes. In the mangrove palm species *Nypa fruticans*, several strains of *Pestalotiopsis* spp. conferred notable tolerance against heavy metals like copper (Cu), lead (Pb), zinc (Zn), and chromium (Cr). It is reported that 1 among the 93 endophytic isolates of *Nypa fruticans* could tolerate heavy metal adulterations to a level of 1000 ppm due to which nipa palm is having significant metallic stress combating strategies (Choo et al. 2015). *Boehmeria nivea* is having endophyte rich rhizosphere like *Bacillus*, *Pseudomonas* and *Cupriavidus* that protects it from excessive concentration of Pb, Cu and Cu

(Jiang et al. 2017). *Penicillium funiculosum, Exophiala pisciphila, Gigapora spp. and Pseudomonas spp*. endophytes effectively overcome the metal stress exhibited by plants by employing metal chelation, improving antioxidant enzyme machinery, altering hormonal status (Friesen et al. 2013; Khan and Lee 2013; Wang et al. 2016; Ma et al. 2019). According to reports, *Penicillium funiculosum* LHL06 secretes gibberellin, which reduces metal toxicity and reprograms the 26 Endophyte-Mediated Host Stress tolerance as a strategy of crop improvement under Cu and Cd stress in soya bean (Khan and Lee 2013). Likewise, endophytes like *Gigaspora* and *Pseudomonas* spp. species can modify the endogenous ethylene levels to increase plant resistance to harmful metals. *Exophiala pisciphila*, a fungal endophyte associated with maize roots, was found to provide resistance to soil cadmium (Cd) toxicity (Friesen et al. 2013). The *E. pisciphila* inoculated plants showed higher expression of genes involved in uptake and translocation of metal mediating chelating in maize. So, increased Cd deposition on maize cell walls, transformation of Cd to less toxic form and antioxidant enzyme activity in response to Cd stress. Furthermore, compared to maize plants devoid endophytes, the plants containing endophytes exhibited excellent growth characteristics and a considerable reduction in Cd-induced phototoxicity levels (Wang et al. 2016). *Pseudomonas stulzeri* produces silver-based crystallic structures that circumvents the toxic effect of metals (Klaus-Joerger et al. 2001).

Moreover, The PGPM have significant role in phytoremediation. They can enhance phytoremediation by plant via fixing of atmospheric nitrogen, mineral solubilization, producing phytohormones and nutrient translocation (Stępniewska and Kuźniar 2013). *P. aeruginosa* inoculation to *Brassica juncea* and *Cucurbita pepo* decreased the Cd uptake, while in chickpea increased plant growth and reduced Ni uptake plants (Sinha and Mukherjee 2008; Tank and Saraf 2009). Thus, communications between PGPM and plants can also compliment the process of metal sequestration by increasing the phyto-remedial capabilities of plants under normal as well as under heavy metal stress.

Enhanced ion production via siderophores

Siderophore producing microorganisms can produce secondary metabolites that encourage plant growth, such as hormones, phosphate solubilization, secondary metabolites, etc. They can pave the way to encourage plant growth in stress conditions such as drought (Breitkreuz et al. 2021). Oxidation states heavy metals are altered by siderophore, rendering them less hazardous in nature (Schalk et al. 2011). Iron is a dynamic supplement for all living organisms. Naturally iron is available as Fe^{3+} and possibly forms insoluble hydroxides which cannot be usable by plants and microbial entities (Rajkumar et al. 2010) Microorganisms discharge iron-binding ligands called ‘‘siderophores,’’ that have high affinity for Fe^{3+} complexes (Gupta and Gopal 2008; Agrawal et al. 2022). *B. subtilis* produces iron-chelating chemicals that increase the amount of nutrients in the soil mediating growth of wheat plant under drought stress (Lastochkina et al. 2020). Under drought conditions, siderophore-producing microorganisms like *Pseudomonas*, improve soil nutrients and other soil activities, such as phosphate and potassium solubilization and siderophore formation (Breitkreuz et al. 2021). Rhizobacteria forms a complex of Fe^{3+} converts it into Fe^{2+} which gets across the cell (Rajkumar et al. 2010). Therefore, under iron-stressed conditions, siderophores producing microorganisms can play the part as iron-solubilizing entity from natural forms (Dimkpa et al. 2009). Microbe based siderophores assist in relieving metal induced stress in plants due to presence of increased metal concentration in the soil (Diels et al. 2002; Schmidt et al. 2005). *Streptomyces tendae* F4 is a Cd-resistant bacterium that produces a number of Cd-binding hydroxamate siderophores. In the absence or presence of (minimum) iron (Fe) concentrations, its production is increased by the metal (Schmidt et al. 2005; Dimkpa et al. 2008). *Azospirillum brasilense* and *Gluconactobacter diazotrophicus* are plant growth promoting bacteria and are reported to produce hydroxamate and catechol siderophore, respectively provides iron nutrition to plants under iron deficiency (Delaporte-Quintana et al. 2020). Toxic heavy metals are trapped by siderophores, which prevents them from impeding the effectiveness of plant cells. Siderophore producing microorganisms can alleviate an iron deficiency. Siderophores tend to maintain iron levels in iron deprived (Braud et al. 2009; Sayyed et al. 2019).

Changes in morphology of root and shoot

Under abiotic stress environments disruption of plant homeostasis occurs that results in decreased plant metabolic functioning, reduced yield, decreased morphological characteristics (Athar and Ahmad 2002; Glick et al. 2007; Bianco and Defez 2009). Formation of phytohormones by microorganisms like gibberellins, indole acetic acid by unknown PGPR’s and ACC deaminase-producing *Klebsiella* spp. in wheat in salt stress and high activity of antioxidant enzyme was reported in *Medicago* plants inoculated by PGPR *Sinorhizobium meliloti* strain as a result of increasing surface area, root length and root surface area that improved nutrient uptake (Bianco et al. 2009; Egamberdieva and Kucharova 2009; Singh et al. 2015; Li et al. 2022a; Neshat et al. 2022). *Pseudomonas extremorientalis, Pseudomonas putida, Pseudomonas aurantiaca* and *Pseudomonas chlororaphis* produced indole acetic acid under saline conditions in wheat plant (Egamberdieva and Kucharova 2009). Inoculation with *Streptomyces* and saline-adapted *Azospirillum* strains considerably developed enhanced the germination rate, dry weight, shoot length and P, Fe, Mn, and N concentrations in wheat plants with saline stress (Nia et al. 2012; Sadeghi et al. 2012). Tomato seeds that have been infected with *Azospirillum brasilens* FT326 considerably enhanced the shoot, root weight, and length of root hairs, due to higher production of phytohormones depending on host specificity (Vaikuntapu et al. 2014). *Pseudomonas fluorescens* have been reported to promote same influence induced by familiar PGPB *Azospirillum brasilens* (Gupta et al. 2015). So, under stressful conditions, ethylene regulates plant homeostasis and leads to growth inhibition including chlorosis, senescence and abscission (Glick et al. 2007; Chen et al. 2022; Liu et al. 2022). But bacterial ACC-deaminase mediated decline of ethylene precursor ACC depresses the concentration of ethylene in roots of plant, thereby relieving its repression and promoting plant growth (Kang et al. 2010).

Volatile organic substances

Volatile organic compounds (VOCs) are small molecular weight (< 300 g mol^{-1}) signaling based molecules that modulates physiological processes of plants and diffuse through the air, water and soil (Audrain et al. 2015; Kanchiswamy et al. 2015; Fincheira et al. 2021; Song et al. 2022). VOCs released from microorganisms in a certain range of scales depending on the living environment and heterogeneity of soil that can act as stimuli to activate the cascade of signals, which controls the physiological processes of plant (Bailly and Weisskopf 2012; Kai et al. 2016; Maheshwari et al. 2021). From past few years, PGPR's role have been deciphered in abiotic stress tolerance (Kumar et al. 2021; Lazazzara et al. 2022). *Bacillus subtilis* based VOCs are known to impart alkaline tolerance in *Arabidopsis thaliana* (Zhang et al. 2010). Wheat seeds treated with *Bacillus thuringiensis* and *Paenibacillus polymyxa B* demonstrated adequate drought resistance. Geranyl acetone, b-pinene and Benzaldehyde like VOCs were produced from these wheat seedlings that tend to mitigate different phases of stress manifestation (Timmusk et al. 2014). Moreover, bacterial VOCs have role in formation of biofilm, which contain exopolysaccharides as main constituent and in turn help to maintain soil moisture content thereby, increasing tolerance against drought in plants (Grover et al. 2011; Naseem and Bano 2014).

Role of different kinds of microbes that are associated with mediating various physiological effects in plants pertaining to abiotic stress tolerance is elucidated in Supplementary Table 1.

Higher K^+/Na^+ ratio

PGPRs have role mediating ion homeostasis in plants under abiotic stress commonly seen under salt stress conditions. Ionic stress causes plants to generate an excessive quantity of Na^+ in the cytosol, which has a deleterious influence on plant cellular physiology in a variety of ways (Hernández et al. 2001; Zhu 2001). PGPR-inoculated plants when grown under salinity conditions have advanced concentration of K^+ ion and there by higher ratio of K^+/Na^+ than non- inoculated plants (Kasotia et al. 2015). Potassium shows a vital part in water stress tolerance, stomatal movements and leaf water status. PGPR may help to prevent salinity-prompted closure of stomata by increasing K^+ concentration (Caravaca et al. 2004). The downregulated K^+ transporter HKT1 expression in roots and upregulation in shoots in *Arabidopsis* was reported by inoculation of *Bacillus subtilis* microbe (Zhang et al. 2010). *Glomus clarum* and *Glomus etunicatum* microbes inoculated mungbean and pepper plants, resulting in increased K^+ in the root and reduced Na^+ in the root and shoot. (Rabie 2005; Kaya et al. 2009).

Brief insights on current scenario of abiotic stress alleviation using multi-omics approaches

The information regarding multi-omics, which is linked to bioinformatics breakthroughs, has increased our knowledge of microbial diversity and its functional aspect in complex ecosystems where microbial community interactions govern plant responses to stressors (Dukare et al. 2022). Meta-omics methods have developed possible tools for delving into microbiota and their behavior in a specific environment (Parray et al. 2022). Abiotic stress management by agricultural genetic modification is critical, yet it is a challenging topic that demands extensive breeding programmes (Tay Fernandez et al. 2022). Marker-aided selection requires knowledge of the genetic areas that influence tolerance qualities, as well as the presence of molecular markers that are intimately linked to them (Mir et al. 2022). Omics approaches help researchers to acquire a better knowledge of well-known plant–microbe relationships (Gupta et al. 2022). These investigations need to be integrated with advanced technologies such as metagenomics, metatranscriptomics, and temporal-spatial mapping of plant responses and microbes colonizing plants. There are several pioneering works in animal microbiota research (Shi et al. 2020) but technological development is still needed for plant microbiota research. For a better knowledge of PGP rhizobacterial populations, metagenomic sequencing at high throughput has also proved to be a very beneficial technique (Kalam et al. 2022). Metagenomics-based diversity profiling and colonization studies can potentially indicate quantitative colonization of a specific host under stress. When combined with meta-transcriptomic analysis, this can provide useful information on stressor-induced changes at functional and taxonomic level of the invading population (Zhou et al. 2022). Plants have been widely investigated in terms of proteomic studies for stress responses (Dong and Chen 2022).

Metabolomics is being utilized more and more to get deeper insights into abiotic stress responses. Metabolomics research has benefited from recent high-throughput breakthroughs in the field of molecular identifying methods (Mashabela et al. 2022). Complex connections in the agroecosystem were revealed by multi-omics and integrated informatics, which showed numerous network modules represented by plant attributes that were heterogeneously related with soil metabolites, minerals, and microbes (Figure 2) (Ichihashi et al. 2020). So, implementation of omics strategies in future to plants as well as its associated microbiome can be the efficient way to tackle the abiotic stresses by them.

Epigenomics

Due to interactions with their environment, plants acquire an epigenetic memory that they pass on to their progeny. Programs for crop development can thus take use of the transgenerational inheritance of epimarks. Epialleles, epigenetic quantitative trait loci and recombinant inbred lines are used in this process to breed for abiotic stress resistance (Gahlaut et al. 2022; Singh et al. 2022c). The prolonged abiotic stress induced the epigenome changes via DNA demethylation and histone remodeling in cold-tolerant genotypes of chickpea and soyabean under cold and salt stress, respectively (Akhter et al. 2021; Sun et al. 2022). Long term exposure of stress leads to methylation of DNA in tolerant cultivar of soybean by inducing expression of some genes like repressor of silencing 1 or by inducing different crosstalk between acetylation and methylation of histones (Liang et al. 2019). Species-specific or conserved epigenetic mechanisms of gene regulation under abiotic stress may exist. By comparing epimarks between species, comparative epigenetics helps us understand the mechanism of epigenetic regulation of biological processes (Zhong 2016). Utilizing naturally occurring epialleles will accelerate the development of alternative plant germplasms with less genetic information.

Transcriptomics

The appropriate model of the gene expression in a target cell or tissue can be provided by transcriptomics, a potent method for quantifying gene expression. The molecular mechanism behind the complicated biological process of a plant response to stress has not yet been fully understood (Wang et al. 2020). Transcriptomics can be used to identify novel genes associated with plant resistance, highlight the complex regulatory network and expression at the entire genome level under stress, and quantitatively quantify changes in plant gene expression at a specific time point in a particular condition (Li et al. 2021). Serial analysis of gene expression (SAGE) and microarrays can now be used

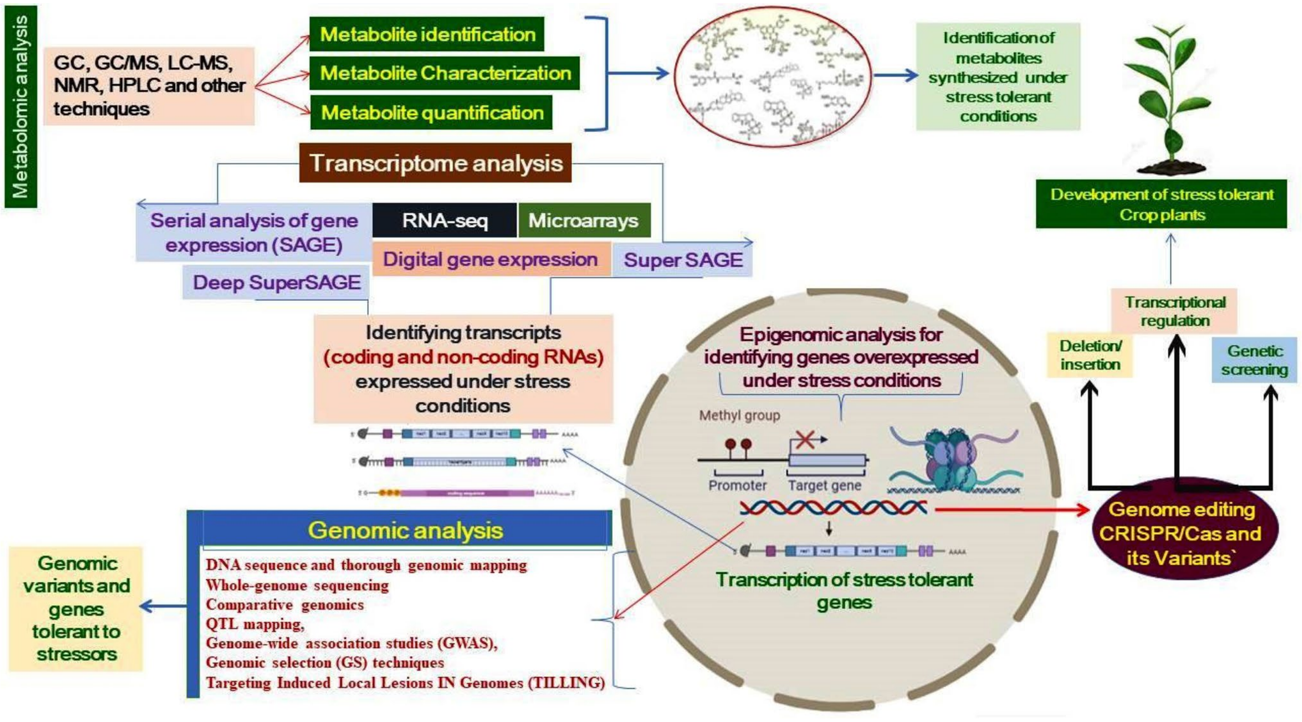

Fig. 2 Demonstration of utilizing omics approaches viz., epigenomics, transcriptomics and genomics for unraveling the resilient genes against the abiotic stressors triggered by plant growth promoting microorganisms and their use to develop stress tolerant crop plants using genome editing technologies

to derive comprehensive transcriptome data because of the advancement of high-throughput technologies. Ribonucleic acid sequencing (RNA-seq) data can be used to detect the differential expression of genes. It is also possible to employ a recently developed method for quantitatively estimating gene expression termed differential gene expression (DGE) (Million and Feyissa 2022). A cost-effective, high-throughput sequencing method called RNA-seq analysis makes it possible to examine a considerable quantity of transcriptome data. In order to comprehend the relevant regulatory mechanisms of plant adaptation to drought, or to increase drought resistance, as well as to clarify the mechanism of plant drought response, transcriptome sequencing is used to study the expression of the entire genome under drought stress (Mishra et al. 2022). After PEG6000 treatment, a total of 11,359 differentially expressed genes (DEGs) were found in sweet potato, of which 7666 were upregulated and 3693 were downregulated (Zhu et al. 2021). Analysis of the leaf and root RNA-sequencing data of *Eucalyptus globulus* revealed a total of 51 *EglWRKY* genes under the condition of cold acclimation with an activation of the expression of numerous *EglWRKY* genes. In the leaf tissues, 11 *EglWRKY* genes were modulated during cold alleviation (Aguayo et al. 2019). Comparative transcriptome study of anthers in rice grown in cold climates under cold stress revealed sucrose and starch metabolism were significant pathways (containing 47 DEGs) (Guo et al. 2019). The common sulphur metabolic pathway is activated under extreme heavy metal stress like aluminium, copper and cadmium according to transcriptome analysis of root toxicity stress in *Arabidopsis thaliana* depending on severity of these stresses (Kusunoki et al. 2018). Both drought-tolerant and drought-sensitive types of soybean have transcriptional alterations that have been documented by comparative transcriptome analysis (Prince et al. 2015). In a transcriptome investigation, Singh et al. discovered potential candidate genes expressed during drought stress in lentil seedlings whereas Pandey et al. discovered dehydration-responsive proteins in chickpea (Pandey et al. 2008; Singh et al. 2017). Using SuperSAGE and deep SuperSAGE, the transcriptomes of chickpeas under drought stress and discovered 80,238 tags representing 17,493 distinct transcripts (Molina et al. 2008). A study of the chickpea root transcriptome revealed the exciting activation of jasmonate in roots under drought conditions (De Domenico et al. 2012).

RNomics

Non-coding RNAs, such as micro ribonucleic acids (miRNAs) and long non-coding RNAs (lncRNAs), are the focus of a novel omics method known as RNomics (Micheel et al. 2021). The miRNAs are thought to be involved in plant related regulation of the stress response. Multiple miRNAs responded to biotic and abiotic stressors, indicating that stress-responsive mechanisms interact with one another (Yung et al. 2022). These miRNAs have a role to develop and react to biotic and abiotic challenges by controlling complex regulatory networks and being involved in a wide variety of biological activities in eukaryotic cells (Šečić et al. 2021). Plant miRNAs are essential regulators of gene expression or silence because they bind to complementary regions on the target messenger RNA (mRNA) to suppress translation or degrade transcripts (Rani and Sengar 2022). These miRNAs are associated with abiotic stress response mechanisms with respect to oxidative stress and impact on DNA in various plant species. Some miRNAs are also activated by a number of conditions in plants, including high temperature, cold, drought, high salt, oxidation, and heavy metals. Upregulating or downregulating the expression of corresponding miRNAs relies on various stimuli and are stress specific in nature (Pagano et al. 2021). The miRNA based response to single or many environmental cues can be as varied like their reactions to plant growth and development. These are known to regulate various aspects of growth and development (Chand Jha et al. 2021). Aux/IAA14 is reported to modulate the miRNA-mediated cold stress response in Arabidopsis. Next-generation sequencing discovered 71 new and 180 known cold-responsive miRNAs (Perea-García et al. 2021). The regulation of maize growth and development under low temperature stress is regulated by miRNA and their potential targets (Aydinoglu 2020). By controlling the GA and ABA signal transduction network, miRNAs demonstrate a substantial superposition or coordinating role in preventing the effects of cold stress (Legnaioli 2013). The first miRNA found in plants includes miR156, which helps plants tolerate high temperatures, is strongly stimulated (Stief et al. 2014). However, miRNAs may have pivotal role in conferring tolerance to drought stress in plants (Singroha et al. 2021). Under salt and wilt stress, several conserved and novel miRNAs linked to gene regulation in chickpea (Kohli et al. 2014). The antioxidant defense system in plants improved their tolerance to salt. The miRNAs might control the scavenging of ROS produced by salinity stress. The miR172 is a confirmed positive regulator of salt tolerance. One of the downstream targets of miR172 is IDS1, which binds to the promoters of ROS scavenging genes to suppress transcription. Thus, during salt stress in cereal crops like rice and wheat, miR172-IDS1 reveals clear regulatory interactions in maintaining ROS homeostasis (Cheng et al. 2021). Long non coding RNA (LncRNAs) are involved in a range of biological processes involving stress tolerance make up a significant share of non-coding RNAs (Jha et al. 2020). Using transcriptome data and the innovative tool plant long non coding RNA prediction (PLncPRO), lncRNAs in plants were reported, and the results showed that the chickpea plant contains a total of 3714 (for drought) and

3457 (for salinity) high-confidence lncRNAs. This tool is based on Machine Learning and utilizes random forest algorithms to classify coding and long non-coding transcripts. The tool is suitable for plants and has better prediction accuracy compared with existing tools (Li et al. 2022b).

Genomics

The study of the structural, functional, and evolutionary components of an organism's genome is referred to as genomics. It means evaluating an organism's complete DNA sequence and thorough genomic mapping (Irion and Nüsslein-Volhard 2022). Whole-genome sequencing helps to find genomic variants and genes related to climate adaptability in wild species of crop plants. It may be directly applicable for using breeding techniques to create crops that are environmentally friendly (Zenda et al. 2021). The development of molecular biology tools has resulted in a plethora of genomic information on legumes. Several species of legumes, including *Medicago truncatula*, *Glycine max*, and *Lotus japonicus*, already had their genomes sequenced. These comparative genomics of legume crops have uncovered important regulatory networks for genes involved in stress adaption and crop productivity (Young et al. 2005; Young and Bharti 2012). The function of protein glycosylation in pulses under stress can be revealed via glycoproteomics. It was discovered that flood stress had a detrimental effect on the N-glycosylation of functional proteins involved in stress control in the case of soybean (Mustafa and Komatsu 2014). An important signaling mechanism in the plant response to abiotic stress is protein phosphorylation. Studies involving phosphoproteomic and glycoproteomic modifications in chickpea and soybean under stress were used (Subba et al. 2013; Showalter et al. 2016). The importance of integrating different omics techniques for abiotic stress tolerance in the model legume crop, soybean, is highlighted by Deshmukh et al. (2014). In terms of the availability of molecular markers, QTL mapping, genome-wide association studies (GWAS), genomic selection (GS) techniques, and transcriptome profiling, significant genomic advancements have been made for abiotic stress tolerance in soybean (Deshmukh et al. 2014). To understand stress responses, microarray studies have been widely used in crop species as well as less-emphasized but nonetheless significant industrially and agriculturally plant species (Ergen et al. 2009; Luo et al. 2010; Loukehaich et al. 2012). High-throughput study of many mutants is made possible by Targeting Induced Local Lesions IN Genomes (TILLING) (McCallum et al. 2000). Salt stress response in legume species was evaluated using TILLING mutants for a particular kinase (De Lorenzo et al. 2009). In order to produce improved varieties with desired features, such as disease resistance, abiotic stress tolerance, or high yield, a process known as marker- assisted selection is used (Collard and Mackill 2008). Genome editing technologies offer a way to introduce precise sequence change, insertion/deletion (indel), and targeted mutation into a range of organisms. The most popular genome editing techniques are clustered regularly interspaced short palindromic repeat (CRISPR)-Cas9 (CRISPR-associated nuclease 9), transcriptional activator-like effector nucleases (TALENs), and zinc finger nucleases (ZFNs) (Satheesh et al. 2019).

Method Literature survey was done by peer-reviewing the international journals and web sources such as Google Scholar/ Academic, pubmed central and Science Direct. In this review, the data pertaining to only various approaches adopted by microbes to mediate abiotic stresses alleviation by microbes is focused.

Conclusion

Microorganisms associated with plants produce different metabolites for combating abiotic stresses and promoting plant growth. Comprehensive understanding of plant–microbe mediated mechanisms for abiotic stress tolerance is necessary to translate the practical use of microbes for plant survival under extreme conditions. This will pave the way for climate-smart agricultural research, which will lead to the advancement and manipulation of beneficial bacteria as the basis of crop bio-fertilizers in the face of changing climatic circumstances, allowing agriculture to become more sustainable. Isolation and characterization of abiotic stress-tolerant microbial variations can help plants cope with stress and might be a viable technique for improving agricultural output in difficult conditions. The extent of microbial stress modification can be dignified as the better proportional effect of beneficial microbes on performance of plant under stressful milieus. However, implementation of genetic techniques serve as signpost in alleviating abiotic stresses via microbial interaction. Numerous omics-based methods, including transcriptomics, proteomics, genomics, phenomics and metabolomics have a vast potential involving the plant-associated microbiome and their collaboration with host plants. It is important to unravel the mechanism and utilization of crop associated beneficial stress tolerant microbes that can be critical to improve food security on global scale. To summarize, we feel that in-depth research on the identification, trait categorization, compatibility evaluation, delivery methods, and impact of introducing microorganisms isolated from varied environmental conditions to agricultural plants for the reduction of abiotic stressors should receive greater attention. Microbiome plant interactions have been proven to have a role in stress reduction across a variety of climatic and edaphic circumstances, thus we need to figure out new functions for microbial metabolites produced in stressed environments.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10725-022-00951-5.

Author contributions NG and SA conceived, NG, SA, and RAM writing and designing. NG, IAW, SHA, SV, JAN and RAM figure making. JAN and RG table making.

Funding The authors have not disclosed any funding.

Declarations

Conflict of interest There are no competing interests declared by the authors.

References

Abd El-Daim IA, Bejai S, Meijer J (2019) Bacillus velezensis 5113 induced metabolic and molecular reprogramming during abiotic stress tolerance in wheat. Sci Rep 9:1–18

Adhya TK, Kumar N, Reddy G et al (2015) Microbial mobilization of soil phosphorus and sustainable P management in agricultural soils. Curr Sci 108:1280–1287

Agrawal S, Kumar V, Singh S, Shahi SK (2022) Gene mediated phytodetoxification of environmental pollutants. In: Kumar V, Shah MP (eds) Phytoremediation technology for the removal of heavy metals and other contaminants from soil and water. Elsevier, Amsterdam, pp 405–433

Aguayo P, Lagos C, Conejera D et al (2019) Transcriptome-wide identification of WRKY family genes and their expression under cold acclimation in *Eucalyptus globulus*. Trees 33:1313–1327

Ahemad M (2012) Implications of bacterial resistance against heavy metals in bioremediation: a review. J Inst Integr Omi Appl Biotechnol 3:39

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. J King Saud Univ 26:1–20

Akhter Z, Bi Z, Ali K et al (2021) In response to abiotic stress, DNA methylation confers epigenetic changes in plants. Plants 10:1096

Akula R, Ravishankar GA (2011) Influence of abiotic stress signals on secondary metabolites in plants. Plant Signal Behav 6:1720–1731

Ali B, Wang X, Saleem MH et al (2022) PGPR-mediated salt tolerance in maize by modulating plant physiology, antioxidant defense, compatible solutes accumulation and bio-surfactant producing genes. Plants 11:345

Arora NK, Fatima T, Mishra I, Verma S (2020) Microbe-based inoculants: role in next green revolution. In: Shukla V, Kumar N (eds) Environmental concerns and sustainable development. Springer, Berlin, pp 191–246

Asaf S, Khan MA, Khan AL et al (2017) Bacterial endophytes from arid land plants regulate endogenous hormone content and promote growth in crop plants: an example of Sphingomonas sp. and Serratia marcescens. J Plant Interact 12:31–38

Asati A, Pichhode M, Nikhil K (2016) Effect of heavy metals on plants: an overview. Int J Appl or Innov Eng Manage 5:56–66

Athar R, Ahmad M (2002) Heavy metal toxicity: effect on plant growth and metal uptake by wheat, and on free living Azotobacter. Water Air Soil Pollut 138:165–180

Audrain B, Farag MA, Ryu C-M, Ghigo J-M (2015) Role of bacterial volatile compounds in bacterial biology. FEMS Microbiol Rev 39:222–233

Aydinoglu F (2020) Elucidating the regulatory roles of microRNAs in maize (*Zea mays* L.) leaf growth response to chilling stress. Planta 251:1–15

Ayub MA, ur Rehman MZ, Umar W et al (2022) Role of glycine betaine in stress management in plants. In: Hossain A, Pamanick B (eds) Emerging plant growth regulators in Agriculture. Elsevier, Amsterdam, pp 335–356

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339. https://doi.org/10.1146/annurev.arplant.59.032607.092752

Bailly A, Weisskopf L (2012) The modulating effect of bacterial volatiles on plant growth: current knowledge and future challenges. Plant Signal Behav 7:79–85

Banchio E, Bogino PC, Santoro M et al (2010) Systemic induction of monoterpene biosynthesis in Origanum × majoricum by soil bacteria. J Agric Food Chem 58:650–654

Bano A, Fatima M (2009) Salt tolerance in *Zea mays* (L). Following inoculation with Rhizobium and Pseudomonas. Biol Fertil Soils 45:405–413

Barka EA, Nowak J, Clément C (2006) Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, Burkholderia phytofirmans strain PsJN. Appl Environ Microbiol 72:7246–7252

Bianco C, Defez R (2009) Medicago truncatula improves salt tolerance when nodulated by an indole-3-acetic acid-overproducing Sinorhizobium meliloti strain. J Exp Bot 60:3097–3107

Bianco C, Imperlini E, Defez R (2009) Legumes like more IAA. Plant Signal Behav 4:763–765

Bilal S, Shahzad R, Khan AL et al (2018) Endophytic microbial consortia of phytohormones-producing fungus *Paecilomyces formosus* LHL10 and bacteria Sphingomonas sp. LK11 to *Glycine max* L. regulates physio-hormonal changes to attenuate aluminum and zinc stresses. Front Plant Sci 9:1273

Braud A, Jézéquel K, Bazot S, Lebeau T (2009) Enhanced phytoextraction of an agricultural Cr-and Pb-contaminated soil by bioaugmentation with siderophore-producing bacteria. Chemosphere 74:280–286

Breitkreuz C, Reitz T, Schulz E, Tarkka MT (2021) Drought and plant community composition affect the metabolic and genotypic diversity of pseudomonas strains in grassland soils. Microorganisms 9:1677

Brooker R, Brown LK, George TS et al (2022) Active and adaptive plasticity in a changing climate. Trends Plant Sci 27:717

Cai G, Li J, Zhou M et al (2022) Compost-derived indole-3-acetic-acid-producing bacteria and their effects on enhancing the secondary fermentation of a swine manure-corn stalk composting. Chemosphere 291:132750

Caravaca F, Figueroa D, Barea JM et al (2004) Effect of mycorrhizal inoculation on nutrient acquisition, gas exchange, and nitrate reductase activity of two Mediterranean-autochthonous shrub species under drought stress. J Plant Nutr 27:57–74

Chand Jha U, Nayyar H, Mantri N, Siddique KHM (2021) Noncoding RNAs in legumes: their emerging roles in regulating biotic/abiotic stress responses and plant growth and development. Cells 10:1674

Chandwani S, Amaresan N (2022) Role of ACC deaminase producing bacteria for abiotic stress management and sustainable agriculture production. Environ Sci Pollut Res 29:22843

Chang P, Gerhardt KE, Huang X-D et al (2014) Plant growth-promoting bacteria facilitate the growth of barley and oats in salt-impacted soil: implications for phytoremediation of saline soils. Int J Phytoremediat 16:1133–1147

Chen H, Bullock DA, Alonso JM, Stepanova AN (2022) To fight or to grow: the balancing role of ethylene in plant abiotic stress responses. Plants 11:33

Cheng X, He Q, Tang S et al (2021) The miR172/IDS1 signaling module confers salt tolerance through maintaining ROS homeostasis in cereal crops. New Phytol 230:1017–1033

Choo J, Sabri NBM, Tan D et al (2015) Heavy metal resistant endophytic fungi isolated from Nypa fruticans in Kuching Wetland National Park. Ocean Sci J 50:445–453

Choudhary S, Wani KI, Naeem M et al (2022) Cellular responses, osmotic adjustments, and role of Osmolytes in providing salt stress resilience in higher plants: polyamines and nitric oxide crosstalk. J Plant Growth Regul. https://doi.org/10.1007/s00344-022-10584-7

Collard BCY, Mackill DJ (2008) Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. Philos Trans R Soc B Biol Sci 363:557–572

Creus CM, Sueldo RJ, Barassi CA (2004) Water relations and yield in Azospirillum-inoculated wheat exposed to drought in the field. Can J Bot 82:273–281

da Silva AV, da Silva MK, Sampaio EBT et al (2022) Benefits of plant growth-promoting symbiotic microbes in climate change era. In: Kumar A, Singh J (eds) Microbiome under changing climate. Elsevier, Amsterdam, pp 85–113

Dardanelli MS, de Cordoba FJF, Espuny MR et al (2008) Effect of Azospirillum brasilense coinoculated with Rhizobium on Phaseolus vulgaris flavonoids and nod factor production under salt stress. Soil Biol Biochem 40:2713–2721

De Domenico S, Bonsegna S, Horres R et al (2012) Transcriptomic analysis of oxylipin biosynthesis genes and chemical profiling reveal an early induction of jasmonates in chickpea roots under drought stress. Plant Physiol Biochem 61:115–122

Defez R, Esposito R, Angelini C, Bianco C (2016) Overproduction of indole-3-acetic acid in free-living rhizobia induces transcriptional changes resembling those occurring in nodule bacteroids. Mol Plant-Microbe Interact 29:484–495

De Lorenzo L, Merchan F, Laporte P et al (2009) A novel plant leucine-rich repeat receptor kinase regulates the response of Medicago truncatula roots to salt stress. Plant Cell 21:668–680

De Zelicourt A, Al-Yousif M, Hirt H (2013) Rhizosphere microbes as essential partners for plant stress tolerance. Mol Plant 6:242–245

Delaporte-Quintana P, Lovaisa NC, Rapisarda VA, Pedraza RO (2020) The plant growth promoting bacteria gluconacetobacter diazotrophicus and *Azospirillum brasilense* contribute to the iron nutrition of strawberry plants through siderophores production. Plant Growth Regul 91:185

Deshmukh R, Sonah H, Patil G et al (2014) Integrating omic approaches for abiotic stress tolerance in soybean. Front Plant Sci 5:244

Diels L, Van der Lelie N, Bastiaens L (2002) New developments in treatment of heavy metal contaminated soils. Rev Environ Sci Biotechnol 1:75–82

Dimkpa CO, Svatoš A, Dabrowska P et al (2008) Involvement of siderophores in the reduction of metal-induced inhibition of auxin synthesis in Streptomyces spp. Chemosphere 74:19–25

Dimkpa CO, Merten D, Svatoš A et al (2009) Metal-induced oxidative stress impacting plant growth in contaminated soil is alleviated by microbial siderophores. Soil Biol Biochem 41:154–162

Dissanayake BM, Staudinger C, Munns R et al (2022) Distinct salinity-induced changes in wheat metabolic machinery in different root tissue types. J Proteomics 256:104502

Dong Y, Chen C (2022) Comprehensive Profiling of Paper Mulberry (Broussonetia papyrifera) crotonylome reveals the significance of lysine crotonylation in Young Leaves. Int J Mol Sci 23:1173

Dukare A, Mhatre P, Maheshwari HS et al (2022) Delineation of mechanistic approaches of rhizosphere microorganisms facilitated plant health and resilience under challenging conditions. 3 Biotech 12:1–33

Egamberdieva D, Kucharova Z (2009) Selection for root colonising bacteria stimulating wheat growth in saline soils. Biol Fertil Soils 45:563–571

Egamberdieva D, Wirth SJ, Alqarawi AA et al (2017) Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. Front Microbiol 8:2104

Elhindi KM, El-Din AS, Elgorban AM (2017) The impact of arbuscular mycorrhizal fungi in mitigating salt-induced adverse effects in sweet basil (*Ocimum basilicum* L.). Saudi J Biol Sci 24:170–179

Elkoca E, Turan M, Donmez MF (2010) Effects of single, dual and triple inoculations with Bacillus subtilis, Bacillus megaterium and Rhizobium leguminosarum bv. Phaseoli on nodulation, nutrient uptake, yield and yield parameters of common bean (Phaseolus vulgaris l. cv.'elkoca-05'). J Plant Nutr 33:2104–2119

Elnahal ASM, El-Saadony MT, Saad AM et al (2022) The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: a review. Eur J Plant Pathol 162:759

Ergen NZ, Thimmapuram J, Bohnert HJ, Budak H (2009) Transcriptome pathways unique to dehydration tolerant relatives of modern wheat. Funct Integr Genomics 9:377–396

Farrar K, Bryant D, Cope-Selby N (2014) Understanding and engineering beneficial plant–microbe interactions: plant growth promotion in energy crops. Plant Biotechnol J 12:1193–1206

Fedoroff NV, Battisti DS, Beachy RN et al (2010) Radically rethinking agriculture for the 21st century. Science (80-) 327:833–834

Figueiredo MVB, Seldin LFF, de Araujo Mariano RLR (2010) Plant growth promoting rhizobacteria: fundamentals and applications. In: Maheshwari D (ed) Plant growth and health promoting bacteria. Springer, Berlin, pp 21–43

Fincheira P, Quiroz A, Tortella G et al (2021) Current advances in plant-microbe communication via volatile organic compounds as an innovative strategy to improve plant growth. Microbiol Res 247:126726

Friesen ML, Porter SS, Stark SC et al (2013) Microbially mediated plant functional traits. Mol Microb Ecol Rhizosphere 1:87–102

Gahlaut V, Jaiswal V, Kumar S (2022) Whole-genome bisulfite sequencing for detection of DNA methylation in crops. In: Wani SH, Kumar A (eds) Genomics of cereal crops. Springer, Berlin, pp 325–334

Ghosh D, Gupta A, Mohapatra S (2019) Dynamics of endogenous hormone regulation in plants by phytohormone secreting rhizobacteria under water-stress. Symbiosis 77:265–278

Ghosh UK, Islam MN, Siddiqui MN et al (2022) Proline, a multifaceted signalling molecule in plant responses to abiotic stress: understanding the physiological mechanisms. Plant Biol 24:227–239

Glick BR (2005) Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol Lett 251:1–7

Glick BR (2010) Using soil bacteria to facilitate phytoremediation. Biotechnol Adv 28:367–374

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-producing soil bacteria. In: Bakker PAHM, Raaijmakers JM (eds) New perspectives and approaches in plant growth-promoting rhizobacteria research. Springer, Dordrecht, pp 329–339

Gravel V, Antoun H, Tweddel RH (2007) Growth stimulation and fruit yield improvement of greenhouse tomato plants by inoculation with Pseudomonas putida or Trichoderma atroviride: possible role of indole acetic acid (IAA). Soil Biol Biochem 39:1968–1977

Gray EJ, Smith DL (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant–bacterium signaling processes. Soil Biol Biochem 37:395–412

Grover M, Ali SZ, Sandhya V et al (2011) Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World J Microbiol Biotechnol 27:1231–1240

Guo Z, Liu C, Xiao W et al (2019) Comparative transcriptome profile analysis of anther development in reproductive stage of rice in cold region under cold stress. Plant Mol Biol Rep 37:129–145

Gupta A, Gopal M (2008) Siderophore production by plant growth promoting rhizobacteria. Indian J Agric Res 42:153–156

Gupta G, Parihar SS, Ahirwar NK et al (2015) Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. J Microb Biochem Technol 7:96–102

Gupta S, Schillaci M, Roessner U (2022) Metabolomics as an emerging tool to study plant–microbe interactions. Emerg Top Life Sci 6:175

Hacquard S, Spaepen S, Garrido-Oter R, Schulze-Lefert P (2017) Interplay between innate immunity and the plant microbiota. Annu Rev Phytopathol 55:565–589

Hardoim PR, Van Overbeek LS, Berg G et al (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiol Mol Biol Rev 79:293–320

Hassen AI, Bopape FL, Sanger LK (2016) Microbial inoculants as agents of growth promotion and abiotic stress tolerance in plants. Microbial inoculants in sustainable agricultural productivity. Springer, New Delhi, pp 23–36

Hayat R, Ali S, Amara U et al (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60:579–598

Hernández JA, Ferrer MA, Jiménez A et al (2001) Antioxidant systems and O2.–/H2O2 production in the apoplast of pea leaves. Its relation with salt-induced necrotic lesions in minor veins. Plant Physiol 127:817–831

Hossain A, Pamanick B, Venugopalan VK et al (2022) Emerging roles of plant growth regulators for plants adaptation to abiotic stress–induced oxidative stress. In: Hossain A, Pamanick B (eds) Emerging plant growth regulators in agriculture. Elsevier, Amsterdam, pp 1–72

Hu YF, Zhou G, Na XF et al (2013) Cadmium interferes with maintenance of auxin homeostasis in *Arabidopsis* seedlings. J Plant Physiol 170:965–975

Ibrahim HM, El-Sawah AM (2022) The Mode of Integration between Azotobacter and Rhizobium affect plant growth, yield, and physiological responses of pea (*Pisum sativum* L.). J Soil Sci Plant Nutr 22:1238

Ichihashi Y, Date Y, Shino A et al (2020) Multi-omics analysis on an agroecosystem reveals the significant role of organic nitrogen to increase agricultural crop yield. Proc Natl Acad Sci USA 117:14552–14560

Iqbal S, Wang X, Mubeen I et al (2022) Phytohormones trigger drought tolerance in crop plants: outlook and future perspectives. Front Plant Sci. https://doi.org/10.3389/fpls.2021.799318

Irion U, Nüsslein-Volhard C (2022) Developmental genetics with model organisms. Proc Natl Acad Sci USA 119:e2122148119

Izaguirre-Mayoral ML, Lazarovits G, Baral B (2018) Ureide metabolism in plant-associated bacteria: purine plant-bacteria interactive scenarios under nitrogen deficiency. Plant Soil 428:1–34

Jha Y, Subramanian RB, Patel S (2011) Combination of endophytic and rhizospheric plant growth promoting rhizobacteria in Oryza sativa shows higher accumulation of osmoprotectant against saline stress. Acta Physiol Plant 33:797–802

Jha UC, Nayyar H, Jha R et al (2020) Long non-coding RNAs: emerging players regulating plant abiotic stress response and adaptation. BMC Plant Biol 20:1–20

Jiang J, Pan C, Xiao A et al (2017) Isolation, identification, and environmental adaptability of heavy-metal-resistant bacteria from ramie rhizosphere soil around mine refinery. 3 Biotech 7:5

Jiménez-Mejía R, Medina-Estrada RI, Carballar-Hernández S et al (2022) Teamwork to survive in hostile soils: use of plant growth-promoting bacteria to ameliorate soil salinity stress in crops. Microorganisms 10:150

Jurburg SD, Eisenhauer N, Buscot F et al (2022) Potential of microbiome-based solutions for agrifood systems. Nat Food 3:557–560

Kai M, Effmert U, Piechulla B (2016) Bacterial-plant-interactions: approaches to unravel the biological function of bacterial volatiles in the rhizosphere. Front Microbiol 7:108

Kalam S, Anirban B, Podile AR (2022) Difficult-to-culture bacteria in the rhizosphere: the underexplored signature microbial groups. Pedosphere 32:75–89

Kanchiswamy CN, Malnoy M, Maffei ME (2015) Chemical diversity of microbial volatiles and their potential for plant growth and productivity. Front Plant Sci 6:151

Kang BG, Kim WT, Yun HS, Chang SC (2010) Use of plant growth-promoting rhizobacteria to control stress responses of plant roots. Plant Biotechnol Rep 4:179–183

Kasotia A, Varma A, Choudhary DK (2015) Pseudomonas-mediated mitigation of salt stress and growth promotion in Glycine max. Agric Res 4:31–41

Kaur H, Hussain SJ, Kaur G et al (2022) Salicylic acid improves Nitrogen fixation, growth, yield and antioxidant defence mechanisms in chickpea genotypes under salt stress. J Plant Growth Regul 41:2034

Kaya C, Ashraf M, Sonmez O et al (2009) The influence of arbuscular mycorrhizal colonisation on key growth parameters and fruit yield of pepper plants grown at high salinity. Sci Hortic (Amsterdam) 121:1–6

Kazan K (2013) Auxin and the integration of environmental signals into plant root development. Ann Bot 112:1655–1665

Khan AL, Lee I-J (2013) Endophytic penicillium funiculosum LHL06 secretes gibberellin that reprograms Glycine max L. growth during copper stress. BMC Plant Biol 13:1–14

Khan AL, Hamayun M, Kim Y-H et al (2011) Gibberellins producing endophytic aspergillus fumigatus sp. LH02 influenced endogenous phytohormonal levels, isoflavonoids production and plant growth in salinity stress. Process Biochem 46:440–447

Khan MIR, Asgher M, Khan NA (2014) Alleviation of salt-induced photosynthesis and growth inhibition by salicylic acid involves glycinebetaine and ethylene in mungbean (*Vigna radiata* L.). Plant Physiol Biochem 80:67–74

Khan MIR, Reddy PS, Ferrante A, Khan NA (2019) Plant signaling molecules: role and regulation under stressful environments. Woodhead Publishing, Sawston

Khedr RA, Sorour SGR, Aboukhadrah SH et al (2022) Alleviation of salinity stress effects on agro-physiological traits of wheat by auxin, glycine betaine, and soil additives. Saudi J Biol Sci 29:534–540

Khoshru B, Mitra D, Khoshmanzar E et al (2020) Current scenario and future prospects of plant growth-promoting rhizobacteria: an economic valuable resource for the agriculture revival under stressful conditions. J Plant Nutr 43:3062–3092

Klaus-Joerger T, Joerger R, Olsson E, Granqvist C-G (2001) Bacteria as workers in the living factory: metal-accumulating bacteria and their potential for materials science. TRENDS Biotechnol 19:15–20

Kohler J, Hernández JA, Caravaca F, Roldán A (2008) Plant-growth-promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. Funct Plant Biol 35:141–151

Kohli D, Joshi G, Deokar AA et al (2014) Identification and characterization of wilt and salt stress-responsive microRNAs in chickpea through high-throughput sequencing. PLoS ONE 9:e108851

Koussevitzky S, Suzuki N, Huntington S, Armijo L, Sha W, Cortes D, Shulaev V, Mittler R (2008) Ascorbate peroxidase 1 plays a key role in the response of Arabidopsis thaliana to stress combination. J Biol Chem 283:34197–34203

Kubicek CP, Herrera-Estrella A, Seidl-Seiboth V, Martinez DA, Druzhinina IS, Thon M, Zeilinger S, Casas-Flores S, Horwitz BA, Mukherjee PK, Mukherjee M (2011) Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of Trichoderma. Genome Biol 12:1–15

Kudoyarova GR, Melentiev AI, Martynenko EV et al (2014) Cytokinin producing bacteria stimulate amino acid deposition by wheat roots. Plant Physiol Biochem 83:285–291

Kumar P, Sharma K, Saini L, Dey SR (2021) Role and behavior of microbial volatile organic compounds in mitigating stress. In: Kumar A, Singh J (eds) Volatiles and metabolites of microbes. Elsevier, Amsterdam, pp 143–161

Kumar A, Kumar N, Yadav N et al (2022) Microbe-mediated amelioration of salinity stress in crops. In: Vaishnav A, Arya S (eds) Plant stress mitigators. Springer, Berlin, pp 429–450

Kumawat KC, Nagpal S, Sharma P (2022) Potential of plant growth-promoting rhizobacteria-plant interactions in mitigating salt stress for sustainable agriculture: a review. Pedosphere 32:223–245

Kusunoki K, Kobayashi Y, Kobayashi Y, Koyama H (2018) Comparative characterization of aluminum responsive transcriptome in *Arabidopsis* roots: comparison with other rhizotoxic ions at different stress intensities. Soil Sci Plant Nutr 64:469–481

Lastochkina O, Garshina D, Ivanov S et al (2020) Seed priming with endophytic Bacillus subtilis modulates physiological responses of two different *Triticum aestivum* L. cultivars under drought stress. Plants 9:1810

Lata R, Chowdhury S, Gond SK, White JF Jr (2018) Induction of abiotic stress tolerance in plants by endophytic microbes. Lett Appl Microbiol 66:268–276

Latef AAHA, Hashem A, Rasool S et al (2016) Arbuscular mycorrhizal symbiosis and abiotic stress in plants: a review. J Plant Biol 59:407–426

Lazazzara V, Avesani S, Robatscher P et al (2022) Biogenic volatile organic compounds in the grapevine response to pathogens, beneficial microorganisms, resistance inducers, and abiotic factors. J Exp Bot 73:529–554

Legnaioli T (2013) Novel mechanisms and transcription factors involved in the control of stomatal behaviour in Arabidopsis thaliana/Nuevos mecanismos y factores de transcripción involucrados en el control del comportamiento estomático en Arabidopsis thaliana. Universitat de Barcelona, Barcelona

Li C, Wang Z, Nong Q et al (2021) Physiological changes and transcriptome profiling in *Saccharum spontaneum* L. leaf under water stress and re-watering conditions. Sci Rep 11:1–14

Li B, Zhang C, Qi M et al (2022) Effects of plant growth-promoting rhizobacteria on uptake and utilization of phosphorus and root architecture in apple seedlings under water limited regimes. Int J Appl Exp Biol 1:1–8

Li J, He H, Li Y et al (2022) Role of long non-coding RNA in plant responses to abiotic stresses. Acta Physiol Plant 44:1–13

Liang X, Hou X, Li J et al (2019) High-resolution DNA methylome reveals that demethylation enhances adaptability to continuous cropping comprehensive stress in soybean. BMC Plant Biol 19:1–17

Liu D, Lian B, Dong H (2012) Isolation of Paenibacillus sp. and assessment of its potential for enhancing mineral weathering. Geomicrobiol J 29:413–421

Liu Y, Shi Z, Yao L et al (2013) Effect of IAA produced by Klebsiella oxytoca Rs-5 on cotton growth under salt stress. J Gen Appl Microbiol 59:59–65

Liu Z, Hartman S, van Veen H et al (2022) Ethylene augments root hypoxia tolerance through amelioration of reactive oxygen species and growth cessation. bioRxiv. https://doi.org/10.1101/2022.01.21.477196

Lopes MJ, dos Dias-Filho S, Gurgel MB (2021) Successful plant growth-promoting microbes: inoculation methods and abiotic factors. Front Sustain Food Syst 5:606454

Loukehaich R, Wang T, Ouyang B et al (2012) SpUSP, an annexin-interacting universal stress protein, enhances drought tolerance in tomato. J Exp Bot 63:5593–5606

Lucena C, Wang J (2022) Beneficial microbes and the interconnection between crop mineral nutrition and induced systemic resistance. Front Plant Sci. https://doi.org/10.3389/fpls.2021.790616

Lugan R, Niogret M, Leport L et al (2010) Metabolome and water homeostasis analysis of Thellungiella salsuginea suggests that dehydration tolerance is a key response to osmotic stress in this halophyte. Plant J 64:215–229

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Luo M, Liu J, Lee RD et al (2010) Monitoring the expression of maize genes in developing kernels under drought stress using oligo-microarray. J Integr Plant Biol 52:1059–1074

Ma Y, Rajkumar M, Zhang C, Freitas H (2016) Beneficial role of bacterial endophytes in heavy metal phytoremediation. J Environ Manage 174:14–25

Ma C, Zhang J, Yuan J et al (2019) Differential expression of microRNAs are responsive to drought stress and exogenous methyl jasmonate in wheat (Triticum aestivum). Int J Agric Biol 22:475–486

Maheshwari HS, Bharti A, Agnihotri R et al (2021) Combating the abiotic stress through Phytomicrobiome Studies. Phytomicrobiome Interact Sustain Agric. https://doi.org/10.1002/9781119644798.ch4

Marulanda A, Azcón R, Chaumont F et al (2010) Regulation of plasma membrane aquaporins by inoculation with a Bacillus megaterium strain in maize (*Zea mays* L.) plants under unstressed and salt-stressed conditions. Planta 232:533–543

Mashabela MD, Piater LA, Dubery IA et al (2022) Rhizosphere tripartite interactions and PGPR-Mediated metabolic reprogramming towards ISR and plant priming: a metabolomics review. Biology (Basel) 11:346

Mathur P, Tripathi DK, Baluska F, Mukherjee S (2022) Molecular mechanisms of auxin mediated regulation of heavy metal and metalloid stress in plants. Environ Exp Bot 196:104796

Mazahar S, Umar S (2022) Soil potassium availability and role of microorganisms in influencing potassium availability to plants. In: Iqbal N, Umar S (eds) Role of potassium in abiotic stress. Springer, Singapore, pp 77–87

McCallum CM, Comai L, Greene EA, Henikoff S (2000) Targeting induced local lesions in genomes (TILLING) for plant functional genomics. Plant Physiol 123:439–442

Meena KK, Sorty AM, Bitla UM et al (2017) Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. Front Plant Sci 8:172

Mendes R, Kruijt M, De Bruijn I et al (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science (80-) 332:1097–1100

Micheel J, Safrastyan A, Wollny D (2021) Advances in non-coding RNA sequencing. Non-coding RNA 7:70

Million M, Feyissa T (2022) RNA-seq as an effective tool for modern transcriptomics, a review-based study. J Appl Res Plant Sci 3:236–241

Mir RA, Nazir M, Naik S et al (2022) Utilizing the underutilized plant resources for development of life style foods: putting nutrigenomics to use. Plant Physiol Biochem 171:128–138

Mishra DC, Guha Majumdar S, Budhlakoti N et al (2022) OMICS tools and techniques for study of defense mechanism in plants. In: Kumar RR, Praveen S (eds) Thermotolerance in crop plants. Springer, Singapore, pp 237–250

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mokrani S, Nabti E, Cruz C (2020) Current advances in plant growth promoting bacteria alleviating salt stress for sustainable agriculture. Appl Sci 10:7025

Molina C, Rotter B, Horres R et al (2008) SuperSAGE: the drought stress-responsive transcriptome of chickpea roots. BMC Genomics 9:1–28

Mousavi SB, Sayfzadeh S, Jabbari H et al (2022) Effect of auxin foliar application on seed yield and fatty acids composition of two safflower genotypes under late-season drought. Plant Soil Environ 68:82–88

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Mustafa G, Komatsu S (2014) Quantitative proteomics reveals the effect of protein glycosylation in soybean root under flooding stress. Front Plant Sci 5:627

Nahar K, Hasanuzzaman M, Fujita M (2016) Roles of osmolytes in plant adaptation to drought and salinity. In: Iqbal N, Nazar R (eds) Osmolytes and plants acclimation to changing environment: emerging omics technologies. Springer, Berlin, pp 37–68

Naseem H, Bano A (2014) Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact 9:689–701

Naz I, Bano A, Ul-Hassan T (2009) Isolation of phytohormones producing plant growth promoting rhizobacteria from weeds growing in Khewra salt range, Pakistan and their implication in providing salt tolerance to Glycine max L. Afr J Biotechnol. https://doi.org/10.5897/AJB09.1176

Neshat M, Abbasi A, Hosseinzadeh A et al (2022) Plant growth promoting bacteria (PGPR) induce antioxidant tolerance against salinity stress through biochemical and physiological mechanisms. Physiol Mol Biol Plants 28:347

Nia SH, Zarea MJ, Rejali F, Varma A (2012) Yield and yield components of wheat as affected by salinity and inoculation with Azospirillum strains from saline or non-saline soil. J Saudi Soc Agric Sci 11:113–121

Nikolic B, Schwab, H, Sessitsch A (2011) Metagenomic analysis of the 1-aminocyclopropane-1-carboxylate deaminase gene (acdS) operon of an uncultured bacterial endophyte colonizing Solanum tuberosum L. Arch Microbiol 193:665–676

Noctor G, Reichheld J-P, Foyer CH (2018) ROS-related redox regulation and signaling in plants. In: Vriz S (ed) Seminars in cell & developmental biology. Elsevier, Amsterdam, pp 3–12

Notununu I, Moleleki L, Roopnarain A, Adeleke R (2022) Effects of plant growth-promoting rhizobacteria on the molecular responses of maize under drought and heat stresses: a review. Pedosphere 32:90–106

Nutan KK, Rathore RS, Tripathi AK et al (2020) Integrating the dynamics of yield traits in rice in response to environmental changes. J Exp Bot 71:490–506

Ogbe AA, Finnie JF, Van Staden J (2020) The role of endophytes in secondary metabolites accumulation in medicinal plants under abiotic stress. S Afr J Bot 134:126–134

Ojuederie OB, Babalola OO (2017) Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. Int J Environ Res Public Health 14:1504

Pagano L, Rossi R, Paesano L et al (2021) miRNA regulation and stress adaptation in plants. Environ Exp Bot 184:104369

Pandey A, Chakraborty S, Datta A, Chakraborty N (2008) Proteomics approach to identify dehydration responsive nuclear proteins from chickpea (*Cicer arietinum* L.). Mol Cell Proteomics 7:88–107

Parray JA, Bandh SA, Shameem N (2022) Climate change and microbes: impacts and vulnerability. CRC Press, Boca Raton

Patel J, Khandwal D, Choudhary B et al (2022) Differential Physio-Biochemical and metabolic responses of peanut (*Arachis hypogaea* L.) under multiple abiotic stress conditions. Int J Mol Sci 23:660

Perea-García A, Andrés-Bordería A, Huijser P, Peñarrubia L (2021) The copper-microrna pathway is integrated with developmental and environmental stress responses in *Arabidopsis thaliana*. Int J Mol Sci 22:9547

Pereira SIA, Monteiro C, Vega AL, Castro PML (2016) Endophytic culturable bacteria colonizing *Lavandula dentata* L. plants: isolation, characterization and evaluation of their plant growth-promoting activities. Ecol Eng 87:91–97

Piccoli P, Travaglia C, Cohen A et al (2011) An endophytic bacterium isolated from roots of the halophyte Prosopis strombulifera produces ABA, IAA, gibberellins a 1 and a 3 and jasmonic acid in chemically-defined culture medium. Plant Growth Regul 64:207–210

Porfirio LL, Newth D, Finnigan JJ, Cai Y (2018) Economic shifts in agricultural production and trade due to climate change. Palgrave Commun 4:1–9

Prasch CM, Sonnewald U (2013) Simultaneous application of heat, drought, and virus to *Arabidopsis* plants reveals significant shifts in signaling networks. Plant Physiol 162:1849–1866

Praveen Kumar G, SK MHA, Desai S, Rasul A, (2014) In vitro screening for abiotic stress tolerance in potent biocontrol and plant growth promoting strains of Pseudomonas and Bacillus spp. Int J Bacteriol 2014:6

Prince SJ, Joshi T, Mutava RN et al (2015) Comparative analysis of the drought-responsive transcriptome in soybean lines contrasting for canopy wilting. Plant Sci 240:65–78

Purdy SJ, Maddison AL, Jones LE, Webster RJ, Andralojc J, Donnison I, Clifton-Brown J (2013) Characterization of chilling-shock responses in four genotypes of Miscanthus reveals the superior tolerance of M. × giganteus compared with M. sinensis and M. sacchariflorus. Ann Bot 111:999–1013

Rabie GH (2005) Influence of arbuscular mycorrhizal fungi and kinetin on the response of mungbean plants to irrigation with seawater. Mycorrhiza 15:225–230

Rajkumar M, Ae N, Prasad MNV, Freitas H (2010) Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. Trends Biotechnol 28:142–149

Ramazan S, Nazir I, Yousuf W, John R (2022) Environmental stress tolerance in maize (Zea mays): role of polyamine metabolism. Funct Plant Biol. https://doi.org/10.1071/FP21324

Rani V, Sengar RS (2022) Biogenesis and mechanisms of microRNA-mediated gene regulation. Biotechnol Bioeng 119:685–692

Rawat J, Pandey N, Saxena J (2022) Role of potassium in plant photosynthesis, transport, growth and yield. In: Iqbal N, Umar S (eds) Role of potassium in abiotic stress. Springer, Springer, pp 1–14

Riaz M, Arif MS, Ashraf MA et al (2019) A comprehensive review on rice responses and tolerance to salt stress. In: Hasanuzzaman M, Fujita M (eds) Advances in rice research for abiotic stress tolerance. Elsevier, Amsterdam, pp 133–158

Rolón-Cárdenas GA, Arvizu-Gómez JL, Soria-Guerra RE et al (2022) The role of auxins and auxin-producing bacteria in the tolerance and accumulation of cadmium by plants. Environ Geochem Health 44:3743

Sadeghi A, Karimi E, Dahaji PA et al (2012) Plant growth promoting activity of an auxin and siderophore producing isolate of

Streptomyces under saline soil conditions. World J Microbiol Biotechnol 28:1503–1509

Sah SK, Reddy KR, Li J (2016) Abscisic acid and abiotic stress tolerance in crop plants. Front Plant Sci 7:571

Santos A, de Silveira A, da Bonifacio JAG et al (2018) Antioxidant response of cowpea co-inoculated with plant growth-promoting bacteria under salt stress. Braz J Microbiol 49:513–521

Satheesh V, Zhang H, Wang X, Lei M (2019) Precise editing of plant genomes–prospects and challenges. In: Jain A, Rai V (eds) Seminars in cell & developmental biology. Elsevier, Amsterdam, pp 115–123

Sati D, Pande V, Pandey SC, Samant M (2022) Recent advances in PGPR and molecular mechanisms involved in drought stress resistance. J Soil Sci Plant Nutr. https://doi.org/10.1007/s42729-021-00724-5

Sayyed RZ, Ilyas N, Tabassum B et al (2019) Plausible role of plant growth-promoting rhizobacteria in future climatic scenario. In: Sobti R, Arora N (eds) Environmental biotechnology: for sustainable future. Springer, Singapore, pp 175–197

Scarpeci TE, Zanor MI, Valle EM (2008) Investigating the role of plant heat shock proteins during oxidative stress. Plant Signal Behav 3:856–857

Schalk IJ, Hannauer M, Braud A (2011) New roles for bacterial siderophores in metal transport and tolerance. Environ Microbiol 13:2844–2854

Schmidt A, Haferburg G, Sineriz M et al (2005) Heavy metal resistance mechanisms in actinobacteria for survival in AMD contaminated soils. Geochemistry 65:131–144

Schweiger R, Baier MC, Persicke M, Müller C (2014) High specificity in plant leaf metabolic responses to arbuscular mycorrhiza. Nat Commun 5:1–11

Šečić E, Kogel K-H, Ladera-Carmona MJ (2021) Biotic stress-associated microRNA families in plants. J Plant Physiol 263:153451

Seleiman MF, Al-Suhaibani N, Ali N et al (2021) Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants 10:259

Shah D, Khan MS, Aziz S et al (2022) Molecular and biochemical characterization, antimicrobial activity, stress tolerance, and plant growth-promoting effect of endophytic bacteria isolated from wheat varieties. Microorganisms 10:21

Shahzad R, Waqas M, Khan AL et al (2016) Seed-borne endophytic Bacillus amyloliquefaciens RWL-1 produces gibberellins and regulates endogenous phytohormones of Oryza sativa. Plant Physiol Biochem 106:236–243

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA (2013) Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. Springerplus 2:1–14

Shelp BJ, Bown AW, Zarei A (2017) 4-Aminobutyrate (GABA): a metabolite and signal with practical significance. Botany 95:1015–1032

Sherin G, Aswathi KPR, Puthur JT (2022) Photosynthetic functions in plants subjected to stresses are positively influenced by priming. Plant Stress 4:100079

Shi H, Shi Q, Grodner B, Lenz JS, Zipfel WR, Brito IL, De Vlaminck I (2020) Highly multiplexed spatial mapping of microbial communities. Nature 588:676–681

Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. J Exp Bot 58:221–227

Showalter AM, Keppler BD, Liu X et al (2016) Bioinformatic identification and analysis of hydroxyproline-rich glycoproteins in Populus trichocarpa. BMC Plant Biol 16:1–34

Singh RP, Jha P, Jha PN (2015) The plant-growth-promoting bacterium Klebsiella sp. SBP-8 confers induced systemic tolerance in wheat (Triticum aestivum) under salt stress. J Plant Physiol 184:57–67

Singh D, Singh CK, Taunk J et al (2017) Transcriptome analysis of lentil (Lens culinaris Medikus) in response to seedling drought stress. BMC Genomics 18:1–20

Singh P, Arif Y, Miszczuk E et al (2022a) Specific roles of lipoxygenases in development and responses to stress in plants. Plants 11:979

Singh P, Singh RK, Zhou Y et al (2022b) Unlocking the strength of plant growth promoting Pseudomonas in improving crop productivity in normal and challenging environments: a review. J Plant Interact 17:220–238

Singh P, Tiwari A, Kumar V, Singh AK (2022c) Genetics and epigenetics-role in development of climate resilient crops. Pharma Innov J 11:1957–1960

Singroha G, Sharma P, Sunkur R (2021) Current status of microRNA-mediated regulation of drought stress responses in cereals. Physiol Plant 172:1808–1821

Sinha S, Mukherjee SK (2008) Cadmium–induced siderophore production by a high Cd-resistant bacterial strain relieved cd toxicity in plants through root colonization. Curr Microbiol 56:55–60

Sinha S, Mishra M (2022) Polyamines: metabolism, regulation, and functions in crop abiotic stress tolerance. In: Ansari SA, Ansari MI (eds) Augmenting crop productivity in stress environment. Springer, Singapore, pp 317–344

Slama I, Abdelly C, Bouchereau A et al (2015) Diversity, distribution and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. Ann Bot 115:433–447

Song GC, Jeon J-S, Sim H-J et al (2022) Dual functionality of natural mixtures of bacterial volatile compounds on plant growth. J Exp Bot 73:571–583

Sorty AM, Bitla UM, Meena KK, Singh NP (2018) Role of microorganisms in alleviating abiotic stresses. In: Panpatte DG, Jhala YK (eds) Microorganisms for green revolution. Springer, Berlin, pp 115–128

Srinivasa C, Mellappa G, Patil SM et al (2022) Plants and endophytes–a partnership for the coumarin production through the microbial systems. Mycology 13:243

Stępniewska Z, Kuźniar A (2013) Endophytic microorganisms—promising applications in bioremediation of greenhouse gases. Appl Microbiol Biotechnol 97:9589–9596

Stief A, Altmann S, Hoffmann K et al (2014) Arabidopsis miR156 regulates tolerance to recurring environmental stress through SPL transcription factors. Plant Cell 26:1792–1807

Subba P, Barua P, Kumar R et al (2013) Phosphoproteomic dynamics of chickpea (*Cicer arietinum* L.) reveals shared and distinct components of dehydration response. J Proteome Res 12:5025–5047

Sun M, Yang Z, Liu L, Duan L (2022) DNA methylation in plant responses and adaption to Abiotic stresses. Int J Mol Sci 23:6910

Suzuki S, He Y, Oyaizu H (2003) Indole-3-acetic acid production in Pseudomonas fluorescens HP72 and its association with suppression of creeping bentgrass brown patch. Curr Microbiol 47:138–143

Tank N, Saraf M (2009) Enhancement of plant growth and decontamination of nickel-spiked soil using PGPR. J Basic Microbiol 49:195–204

Tariq A, Ahmed A (2022) Auxins-interkingdom signaling molecules. In: Hano C (ed) Plant hormones: recent advances, new perspectives and applications, vol 3. IntechOpen, London

Tay Fernandez CG, Nestor BJ, Danilevicz MF et al (2022) Expanding gene-editing potential in crop improvement with pangenomes. Int J Mol Sci 23:2276

Timmusk S, Abd El-Daim IA, Copolovici L et al (2014) Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. PLoS ONE 9:e96086

Tiwari P, Bajpai M, Singh LK et al (2020) Phytohormones producing fungal communities: metabolic engineering for abiotic stress tolerance in crops. In: Yadav AN, Mishra S (eds) Agriculturally important fungi for sustainable agriculture. Springer, Berlin, pp 171–197

Tondo ML, Delprato ML, Kraiselburd I et al (2016) KatG, the bifunctional catalase of Xanthomonas citri subsp. citri, responds to hydrogen peroxide and contributes to epiphytic survival on citrus leaves. PLoS ONE 11:e0151657

Trivedi P, Batista BD, Bazany KE, Singh BK (2022) Plant–microbiome interactions under a changing world: responses, consequences and perspectives. New Phytol. https://doi.org/10.1111/nph.18016

Vaikuntapu PR, Dutta S, Samudrala RB et al (2014) Preferential promotion of Lycopersicon esculentum (Tomato) growth by plant growth promoting bacteria associated with tomato. Indian J Microbiol 54:403–412

van Hulten M, Pelser M, Van Loon LC et al (2006) Costs and benefits of priming for defense in *Arabidopsis*. Proc Natl Acad Sci USA 103:5602–5607

Van Oosten MJ, Pepe O, De Pascale S et al (2017) The role of biostimulants and bioeffectors as alleviators of abiotic stress in crop plants. Chem Biol Technol Agric 4:1–12

Vardharajula S, Zulfikar Ali S, Grover M et al (2011) Drought-tolerant plant growth promoting Bacillus spp.: effect on growth, osmolytes, and antioxidant status of maize under drought stress. J Plant Interact 6:1–14

Viterbo A, Landau U, Kim S, Chernin L, Chet I (2010) Characterization of ACC deaminase from the biocontrol and plant growth-promoting agent Trichoderma asperellum T203. FEMS Microbiol Lett 305:42–48

Waadt R, Seller CA, Hsu P-K et al (2022) Plant hormone regulation of abiotic stress responses. Nat Rev Mol Cell Biol 23:680

Walker V, Bertrand C, Bellvert F et al (2011) Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus Azospirillum. New Phytol 189:494–506

Wang C-J, Yang W, Wang C et al (2012) Induction of drought tolerance in cucumber plants by a consortium of three plant growth-promoting rhizobacterium strains. PLoS ONE 7:e52565

Wang J, Li T, Liu G et al (2016) Unraveling the role of dark septate endophyte (DSE) colonizing maize (Zea mays) under cadmium stress: physiological, cytological and genic aspects. Sci Rep 6:1–12

Wang P, Zhao Y, Li Z et al (2018) Reciprocal regulation of the TOR kinase and ABA receptor balances plant growth and stress response. Mol Cell 69:100–112

Wang X, Li N, Li W et al (2020) Advances in Transcriptomics in the response to stress in plants. Glob Med Genet 7:30–34

Wang W, Pang J, Zhang F et al (2022) Salt–responsive transcriptome analysis of canola roots reveals candidate genes involved in the key metabolic pathway in response to salt stress. Sci Rep 12:1–16

Wani ZA, Ashraf N, Mohiuddin T, Riyaz-Ul-Hassan S (2015) Plant-endophyte symbiosis, an ecological perspective. Appl Microbiol Biotechnol 99:2955–2965

Waqas M, Khan AL, Kamran M et al (2012) Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. Molecules 17:10754–10773

Yadav B, Jogawat A, Rahman MS, Narayan OP (2021) Secondary metabolites in the drought stress tolerance of crop plants: a review. Gene Rep 23:101040

Young ND, Bharti AK (2012) Genome-enabled insights into legume biology. Annu Rev Plant Biol 63:283–305

Young ND, Cannon SB, Sato S et al (2005) Sequencing the genespaces of Medicago truncatula and Lotus japonicus. Plant Physiol 137:1174–1181

Yung W, Huang C, Li M, Lam H (2022) Changes in epigenetic features in legumes under abiotic stresses. Plant Genome. https://doi.org/10.1002/tpg2.20237

Zenda T, Liu S, Dong A, Duan H (2021) Advances in cereal crop genomics for resilience under climate change. Life 11:502

Zhang H, Murzello C, Sun Y et al (2010) Choline and osmotic-stress tolerance induced in *Arabidopsis* by the soil microbe Bacillus subtilis (GB03). Mol Plant-Microbe Interact 23:1097–1104

Zhong X (2016) Comparative epigenomics: a powerful tool to understand the evolution of DNA methylation. New Phytol 210:76–80

Zhou C, Ma Z, Zhu L et al (2016) Rhizobacterial strain Bacillus megaterium BOFC15 induces cellular polyamine changes that improve plant growth and drought resistance. Int J Mol Sci 17:976

Zhou L, Xu P, Gong J et al (2022) Metagenomic profiles of the resistome in subtropical estuaries: co-occurrence patterns, indicative genes, and driving factors. Sci Total Environ 810:152263

Zhu J-K (2001) Plant salt tolerance. Trends Plant Sci 6:66–71

Zhu H, Zhou Y-Y, Zhai H et al (2021) Transcriptome profiling reveals insights into the molecular mechanism of drought tolerance in sweetpotato. J Integr Agric 18:9