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Perspectives on the potential application of cyanobacteria in the alleviation of drought and salinity stress in crop plants

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Abstract
Agriculture faces serious constraints due to drought and salinity. Soils under these pressures can result in low productivity, decreasing the farmlands area and a negative impact on the food security. In this context, the cyanobacteria (blue-green algae) can be considered important microorganisms. They are commonly found in rice fields and agricultural soils where they perform important ecological functions. Cyanobacteria improve the soil fertility and productivity of crops through the fixation of atmospheric nitrogen, phosphate solubilization and release of nutrients. Several cyanobacteria also secrete biologically active compounds such as phytohormones, amino acids, polysaccharides and vitamins which help in plant growth promotion. Studies have shown the potential of these compounds in the alleviation of abiotic stress in crop plants. Through an array of physiological, biochemical and molecular mechanisms, the cyanobacteria improve plant growth and development. Therefore, mitigation strategies using cyanobacteria are important in combating the drought and salinity stress. This article discussed the possible outcomes of employing cyanobacteria to regulate the growth and development of plants as an effective way to overcome the drought and salinity stress.

Keywords Agriculture · Cyanobacteria · Abiotic stress · Nitrogen fixation · Plant growth promotion

Introduction

The world population is increasing rapidly and is expected to be about 9 billion by 2050 (Zhang et al. 2015). This will be accompanied by an increase in incidences of land degradation, abiotic stresses and global climate change. All these factors make it more difficult to achieve the agricultural productivity required. Drought stress is considered as one of the most serious threats to agriculture as it can adversely affect agricultural production. Lau and Lennon (2012) observed that long duration drought and extremely dry events are occurring more often due to changes in the mean global temperature and pattern of precipitation. The drought stress creates serious plant developmental problems in more than 50% of the arable lands (Vinocur and Altman 2005; Kasim et al. 2013). Similarly, salinity is also one of the major abiotic stresses for agriculture worldwide. Increasing concentration of salts in the soil leads to wide range of perturbations due to osmotic stress and accumulation of Na^+ and Cl^- ions in plants (Deinlein et al. 2014). Severe reduction in crop production and economic losses due to soil salinization have been reported (Qadir et al. 2014). Drought and salinity also may pose a severe threat to soil microorganisms causing a decline in their population (Lan et al. 2010). This effect is also observed in cyanobacteria that are key components in ecosystems, playing significant role in the biogeochemical cycles involving carbon and nitrogen (Stal 2007). Therefore, the threat due to abiotic stressors such as

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drought and salinity is a serious concern for modern agriculture due to decline in the population of microorganisms.

Farming is difficult in land suffering from drought and salinity. Therefore, reclamation of drought and salt affected soil is important in restoring the fertility and productivity of soils. Land reclamation can be achieved by different physical, chemical and biological means. For example, Luo et al. (2018) employed vegetation systems to reclaim saline soils and reclamation of saline soil through organic amendments was attempted by Saifullah et al. (2018). Several chemicals have also been used to reclaim desertified soils (Yang et al. 2007; Lee et al. 2011; Li et al. 2011). To cope with drought stress, resource management practices, shifting of crop calendars and development of drought tolerant varieties have been attempted (Venkateswarlu and Shanker 2009). Drought management involving plant breeding and growth systems take time and is expensive (Evseeva et al. 2019). Recent investigations reveal that microorganisms can help plants to overcome drought and salinity stress. The rhizosphere is where rhizosphere-associated microorganisms perform diverse metabolic activities to enhance soil fertility and plant growth (Dennis et al. 2010). Mustafa et al. (2019) observed the role of beneficial microbes that help plants to cope with drought conditions. Recently, Vurukonda et al. (2016) reviewed the enhancement of drought stress tolerance in plants through the application of plant growth promoting bacteria that colonize the rhizosphere and benefit root growth. Therefore, microbe assisted/mediated technologies are considered to be better options to minimize stress as these techniques are less time consuming and cost effective.

Cyanobacteria are important constituents of the soil microbial community. Some cyanobacteria fix atmospheric nitrogen and release it to soil (Issa et al. 2014). In addition to nitrogen fixation, the ability of cyanobacteria to solubilize phosphate has been reported (Latha et al. 1992). Excretion of phytohormones such as auxins and gibberellins, vitamins and amino acids by the cyanobacteria has been shown to have positive consequences on the growth and development of plants (Roger and Reynaud 1982; Rodríguez et al. 2006; Seyed et al. 2012; Shariatmadari et al. 2013). The processes of nitrogen fixation and production and excretion of metabolites play an important role in plant growth and development. Lau and Lennon (2011) observed that the microbial population below the ground level influenced plant traits through mitigation of the effects of abiotic stress. However, most of the work carried out on cyanobacteria is regarding their biofertilizer potential and very little attention has been paid to elucidate the beneficial role of cyanobacteria on crop plants. Therefore, the present review is aimed to highlight cyanobacteria-mediated plant growth and regulation including abiotic stress mitigation in crop plants.

Cyanobacteria and their diversity

Cyanobacteria, also known as blue-green algae are Gram negative prokaryotes that grow under photoautotrophic conditions. They are primary producers of the ecosystem and play a key role in shaping the microbial diversity and community structure (Yang et al. 2016). Their structural organization ranges from simple unicellular forms to complex filamentous forms that possess a variety of highly differentiated cell types, but they reproduce by simple vegetative means. Among the filamentous forms, some are capable of simple branching whereas some are multicellular and truly branching. Several filamentous forms exhibit cellular differentiation into vegetative cells and specialized cells known as heterocysts having the ability to fix atmospheric nitrogen (Waterbury 2006). The vegetative cells perform photosynthesis whereas nitrogen fixation is performed by the heterocysts. The cyanobacteria also can thrive in extreme environments such as deserts (Rossi et al. 2017; Roncero-Ramos et al. 2019). Recently, Gaysina et al. (2019) reviewed the diversity of cyanobacteria from different climatic zones such as temperate, tropical and polar regions. Another interesting aspect of the cyanobacteria is their ability to establish symbiotic associations with a wide range of hosts (Adams et al. 2013). The host in the symbiotic association provides a unique environment and nutrition to the cyanobacteria whereas the cyanobacteria supply fixed nitrogen to the host plants. Symbiotic association between cyanobacteria and fungi (Tschermak-Woess 1988), bryophytes (Meeks 2003), pteridophytes (Plazinski et al. 1990), gymnosperms (Costa and Lindblad 2002) and angiosperms (Bergman 2002) are well known. Epiphytic growth of cyanobacteria also has been observed on the bark of trees and leaves (Rigonato et al. 2012; Ambika and Krishnamurthy 2019). The cyanobacteria are clearly versatile organisms and therefore have been exploited in research for agricultural, medicinal and industrial applications.

Cyanobacteria are divided into five orders (Rippka et al. 1979). The Chroococcales consists of unicellular or colonial forms, pseudo-filaments without trichomes and which reproduce by binary fission. Unicellular or colonial lithophytes, epiphytes or epilithic exhibiting polarity and reproduce by endospores and exospores are placed in the order Chaemosiphonales. Cyanobacterial forms which are heterotrichous, filamentous without heterocyst and which reproduce by endospores belong to the order Pleurocapsales. The Nostocales are characterized by non-heterotrichous and heterocystous filamentous forms often showing false branching and reproduction by hormogonia, hormocysts, planococci and akinetes. The Stigonematales consists of heterotrichous filamentous forms mostly with heterocysts and reproduce by akinites. The rich biodiversity of the cyanobacteria in various environments such as marine waters, brackish waters, soda lakes, deserts, hypersaline environments, polar regions, fresh waters, paddy fields and soil has been described by Thajuddin and Subramaniyan (2005). Dash et al. (2017a) also have reported the dominance of unicellular cyanobacterial forms such as *Aphanothece* sp. This widespread colonization is promoted by the availability of nutrients, water, high level of carbon and the ideal temperature (Kondo and Yasuda 2003). Diversity studies conducted in the rice fields of Eastern Uttar Pradesh, India revealed the presence of diverse forms of cyanobacteria and the majority belonging to the order Nostocales (Srivastava et al. 2009). Bhatnagar et al. (2008) reported the dominance of heterocystous and non heterocystous cyanobacterial strains such as *Phormidium*, *Oscillatoria*, *Lyngbya*, *Nostoc*, *Scytonema* and *Calothrix* in Thar desert, India. Culture-dependent studies conducted by Patel et al. (2019) on the dry mats collected from the subtropical region of Rann of Kutch suggested the dominance of unicellular forms such as *Euthece* and *Halothece* sp. Desert crusts from Utah's Colorado Plateau showed significant differences in the community structure of cyanobacteria (Garcia-Pichell et al. 2001). Several other studies conducted in Mexico and USA showed the dominance of similar cyanobacterial forms in desert crusts (Fernandes et al. 2018). Cyanobacteria have also been observed in the phyllosphere region of rice plants (Dhankar et al. 2021). Venkatachalam et al. (2016) reported the presence of several diverse forms of unicellular and filamentous non-heterocystous cyanobacteria in the phyllosphere region of rice (Pusa Basmati cv. 1509) having a role in plant growth promotion. They constitute one of the dominant microbial communities in the rice fields and in the tropical paddy field ecosystem, a huge population of diazotrophic cyanobacteria such as *Anabaena*, *Nostoc*, *Tolypothrix* and *Aulosira* has been reported (Dash et al. 2016; Dash et al. 2017b).

Cyanobacteria exhibit plant promoting traits

In general, compounds produced by cyanobacteria are important for the growth and development of plants. The ubiquitous presence of cyanobacteria in the soil rhizosphere of a number of crops is therefore important in relation to plant growth and development. An array of metabolites produced by the cyanobacteria can also help in the regulation of plant growth under abiotic stress conditions induced by drought and salinity. Since use of conventional technologies alone on the mitigation of abiotic stress has not been successful, the exploitation of beneficial cyanobacteria in the crop rhizosphere can also be considered an important strategy in the alleviation and mitigation of abiotic stresses such as drought and salinity. The cyanobacteria have several unique attributes which confer them the potential to be employed as bio-inoculants for the mitigation of salinity/drought in plants (Table 1).

Katoh et al. (2012) observed that the enhancement in growth and rooting of several vegetable plants was due to germination promoting compounds released by the cyanobacteria. Apart from enriching the nutrient content of the soil, cyanobacteria have been reported to release various biologically active compounds extracellularly which act as signaling molecules in plant growth promotion. These compounds consist of phytohormones, proteins, vitamins, amino acids carbohydrates and polysaccharides (Rodgers et al. 1979; Selykh and Semenova 2000; Sergeeva et al. 2002; Hussain et al. 2013; Delattre et al. 2016; Singh et al. 2017). Cyanobacteria have shown the ability to accumulate and secrete phytohormones. Endogenous indole-3-acetic acid (IAA) production has been detected in cyanobacteria (Mazhar et al. 2013). In rice, inoculation of the cyanobacteria enhanced the IAA levels and increased the salinity tolerance (Singh et al. 2011). Phytohormones such as indole-3 acetic acid (IAA), indole-3 butyric acid (IBA) along with free volatile fatty acids from the wet cyanobacterial biomass promoted the plant growth in cucumber (Gayathri et al. 2017). In general, phytohormone production has been reported mostly from cyanobacteria isolated from crop fields. However, *Arthrospira platensis*, which is not a common inhabitant of agricultural fields exhibit the potential of IAA production and enhanced the root and plant growth (Mehboob et al. 2010). Through the excretion of phytohormones, the microbes can change the endogenous hormone balance of the host plants and promote plant cell division, growth and nutrient release (Glick et al. 1999). High performance liquid chromatography (HPLC) of the extracts of cyanobacterial species such as *Nostoc carneum*, *Nostoc punctiforme* and *Wollea vaginicola* showed their ability to produce Indole-3-acetic acid, Indole-3-propionic acid and Indole-3-butyric acid and a significant and positive correlation was observed between these hormones and growth of *Matricaria chamomilla* plants (Zarezadeh et al. 2020). In addition to auxins, cyanobacteria also are known to produce cytokinins. Osman et al. (2010) reported the occurrence of cytokinin production from several cyanobacterial strains. Cyanobacterial species such as *Oscillatoria angustissima*, *Cylindrospermum* sp. and *Anabaenopsis* sp. have been reported to produce gibberellin-like substances (Tsavkelova et al. 2006). Yang et al. (2009) observed that the phytohormones are able to enhance the resistance of the plants to environmental stresses. Further, the role of phytohormones in the induction of genes for the synthesis of enzymes, pigments and metabolites have been reported (Bari and Jones 2009; Shan et al. 2012). Singh (2014) highlighted

Table 1 Inherent attributes of cyanobacteria for their exploitation in the mitigation of drought/salinity stress

Property	Mechanism	Cyanobacteria	References
Morphological			
Extracellular sheath	Absorption and water holding, resistance to desiccation, absorption of UV radiation	*Chlorogleopsis* PCC 6912, *Phormidium uncinatum*, *Gleocapsa*sp, *Nostoc commune*	Schrader et al. (1982); Peat and Potts (1987); Garcia-Pichel et al. (1993); Hoiczyk (1998)
Production of extracellular polysaccharides	Soil aggregation and water availability	*Leptolyngbya ohadii*	Arora et al. (2010); Mugnai et al. (2018a)
Ionic adjustments			
Influx and efflux of sodium ions	Turgour/ ionic adjustments, exclusion of sodium ions	*Anabaena torulosa*, *Anabaena* sp. strain L-31, *Synechococcus* sp. PCC 6714	Reed et al. (1984b); Apte et al. (1987)
Active efflux of sodium and transport mechanisms involving Na^+/H^+ antiporter	Removal of sodium and maintenance of low intracellular sodium content	*Synechocystis* PCC 6803	Elanskaya et al. (2002); Tsunekawa et al. (2009); Berry et al. (2003)
Accumulation of potassium ions	Increased cellular content of potassium ions triggers the biosynthesis of osmolytes and also for several processes	*Synechocystis* PCC 6803, *Anabaena torulosa*	Matsuda et al. (2004); Apte and Alahari (1994)
High affinity K^+ uptake system	Turgour induced rapid influx of potassium ions and maintenance of K^+/Na^+ ratio	*Synechocystis* PCC 6803	Nanatani et al. (2015)
Osmotic adjustments			
Accumulation of compatible solutes (Quarternary ammonium compounds, sugars, glycine betaine)	Protection of the cell membrane system and cellular enzymes	*Microcystis firma*, *Anabaena variabilis and Synechocystis aquatilis*, *Rivularia atra*, *Aphanothece halophytica*, *Coccochloris elabens*	Erdmann (1983); Reed and Stewart (1983); Reed et al. (1984a); Waditee et al. (2002)
Synthesis of glucosyl glycerol due to salinity	As compatible solutes	*Synechocystis* PCC 6803	Hagemann 2011: Kirsch et al. (2019)
Synthesis osmotic stress/water stress proteins	Osmotic protection and modification of osmotic tolerance	*Anabaena* sp., *Nostoc* sp.	Fulda et al. (1999)
Antioxidant defence			
Increase in the level of proline, SOD, APX, CAT, GR	Scavenging and detoxifying of harmful free radicals	*Anabaena* sp.	Yadav et al. (2016)
Plant growth promoting attributes			
Production of growth hormones, vitamins, peptides	These compounds help in plant growth promotion	*Chroococcidiopsis* sp., *Anabaena* sp., *N. muscorum*, *Hapalosiphon* sp.,	Misra and Kaushik (1989b); Adam (1999); Hussain and Hasnain (2011)

the positive role of signalling molecules produced by the cyanobacteria in bringing about qualitative and quantitative changes in the phytochemical composition of plants. The phytohormone, abscisic acid (ABA) acts as a signalling molecule and plays an important role in plant response to abiotic stresses. Hartung (2010) reported the production of abscisic acid (ABA) in cyanobacteria exposed to stress conditions induced by salinity. Signalling molecules such as jasmonates and their derivatives are also important in the regulation of several physiological processes related to growth, development and abiotic stress tolerance in plants (Kazan 2015). Jasmonic acid production has been reported in several cyanobacteria such as *Anabaena*, *Calothrix*, *Cylindrospermum*, *Nostoc*, *Scytonema, Spirulina* and *Synechococcus* sp. (Ueda et al. 1991; Tsavkelova et al. 2006). However, Han (2017) reported that further studies are needed to confirm the presence of jasmonates in cyanobacteria. Excretion of phytohormones such as auxins and gibberellins by the cyanobacteria has been reported to have positive consequences on the growth and development of plants (Rodríguez et al. 2006; Hussain and Hasnain 2011; Gayathri et al. 2015). The role of signaling molecules produced by cyanobacteria is therefore crucial in the management of abiotic stresses.

The cyanobacterial exudates have also been reported to contain amino acids (Karthikeyan et al. 2007), vitamins (Borowitzka 1988) and antibiotics (Gromov et al. 1991) which aid in plant growth promotion. The cellular as well as extracellular products of *Hapalosiphon fontinalis* and *Nostoc muscorum* increased the length of coleoptiles and radicle of rice seedlings due to the presence of amino acids (Misra and Kaushik 1989a, b). Another important secondary metabolite of cyanobacterial origin are the peptides and their constituent amino acids (Sivonen et al. 2010). These peptides are synthesized by non-ribosomal peptide synthetase (NRPs), polyketides (PK) or hybrid non-ribosomal peptide synthetase/polyketide synthase pathways (Kehr et al. 2011). The structural elucidation of a number of cyanobacterial peptides has been carried out (Welker and Döhren 2006; Fidor et al. 2019). Filtrates obtained from *N. muscorum* enhanced the growth and development of crops probably due to amino acids and peptides (Adam 1999). Foliar application of cyanobacteria as biofertilizer enhanced the photosynthetic performance and growth of *Salix viminalis* plants (Grzesik et al. 2017).

Vitamins also play a significant role in the growth and development of plants and the cyanobacteria are known to be a rich source of vitamins (Abed et al. 2009). In rice seedlings, enhancement in the root growth obtained with the application of extract of *Calothrix muscicola* was found to be at par with the results obtained with pure cyanocobalamin (Vitamin B12) and folic acid (Venkataraman and Neelakantan 1967). Several vitamins play an important role in the antioxidant defence. The antioxidant defence system of the plants consists of superoxide dismutase, catalase, peroxidase, glutathione reductase and low molecular weight compounds such as ascorbate, glutamine and tocopherols and the cyanobacterial peptides have been reported to stimulate the antioxidant defense system in plants (Chen et al. 2004; Pflugmacher et al. 2007). Under stress conditions, the vitamins such as A, C, E (α-tocopherol) and carotenoids play an important role in scavenging the reactive oxygen species (ROS) and protecting the cells against lipid peroxidation (Havaux et al. 2009; Latifi et al. 2009). Cyanobacteria are rich in pigments such as chlorophyll *a*, carotenoids and phycobiliproteins such as phycocyanin, phycoerythrin and allophycocyanin. Phycocyanin isolated from *Arthrospira* (*Spirulina*) *platensis* enhanced the accumulation of anthocyanin pigment in plants (Rao et al. 1996). Anthocyanin is important in protecting the plants against various abiotic stresses partially due to their powerful antioxidant properties (Ahmed et al. 2014).

Cyanobacterial polysaccharides are present as a mucilaginous external layer around the cell. Ultrastructure and chemical composition of the extracellular sheath in *Phormidium uncinatum* has been studied by Hoiczyk (1998). A number of cyanobacterial species, ranging from unicellular to filamentous and hetrocystous to non-heterocystous forms are known to release soluble polysaccharides into the environment during their growth. Nisha et al. (2007) reported the production of exopolysaccharides (EPS) by several strains of cyanobacteria. The sheath is composed of exopolysaccharide fractions with complex monosaccharide composition and is comprised of proteins, lipids, nucleic acids and secondary metabolites (De Philippis and Vincenzini 1998; Delattre et al. 2016). Although, glucose is the most common monosaccharide, in some cyanobacteria, rhamnose, xylose, arabinose, mannose, fructose and uronic acids are the most dominant monosaccharides (Rossi and De Philippis 2016). At the same time, these compounds are important in soil aggregation and maintaining water availability under desiccated environments (Malamlssa et al. 2001; Arora et al. 2010; Mugnai et al. 2018a). The dominance of cyanobacteria in extreme environments is attributed to the presence the sheath made up of extrapolymeric substances. These attributes are used for their own advantage, allowing them to survive and dominate extreme environments (Di Pippo et al. 2013). Peat and Potts (1987) observed that *N. commune* UTEX 584 subjected to extreme desiccation was able to survive due to the cellular organization. The extracellular sheath in *Gleocapsa* sp. contains photoprotective pigments which help them to survive high rates of desiccation (Garcia-Pichel and Castenholz 1993). Availability of adequate soil moisture and organic content in turn support the growth and survival of plant growth producing rhizobacteria in the plant rhizosphere. Flaibani et al. (1989) reported that exopolysaccharides from cyanobacteria also contribute to reclamation of the desert soils. EPS producing cyanobacteria along with other plant growth producing rhizobacteria may thus help in the reclamation of non-productive soils (Paul and Nair 2008). Importance of extracellular polysaccharides in *Nostoc* sp. in alleviating the salinity stress has been highlighted by Yoshimura et al. (2012). The extracellular polysaccharides released by the cyanobacteria chelates the dissociated sodium ions and thereby reduce the abundance and toxicity of these ions in the rhizosphere, making the soil suitable for the proliferation of root growth and development (Arora et al. 2010). Production of extracellular matrix and compatible solutes by cyanobacterial species such as *Anabaena* and *Nostoc* sp. was found to reduce the problem of soil salinization to a great extent (Li et al. 2019).

The supply and utilization of nitrogen is key to the successful production of rice. Venkataraman (1972) suggested algalization of rice fields in the improvement and maintenance of soil fertility. Most of the beneficial effects of cyanobacteria have been reported in rice plants due to their natural presence in rice field ecosystems (Rodgers et al. 1979; Singh et al. 1985; Fernández Valiente et al. 2000; Whitton 2000; Pereira et al. 2009; Dash et al. 2018). The flooded rice fields provide cyanobacteria a unique niche to grow due to the availability of light, water, nutrients and temperature to maintain/enhance the productivity of the rice fields (Roger et al. 1993). Seasonal and crop stage specific diversity of the cyanobacterial flora was also observed in flooded rice fields (Roger and Kulasooriya 1980; Nayak et al. 2001). Besides organic matter, the cyanobacteria can contribute about 20–30 kg N ha^{-1} to the paddy fields (Issa et al. 2014). Further, the excretion of organic acids and extracellular phosphatases by the cyanobacteria also contribute to the mobilization of inorganic phosphates (Rai and Sharma 2006). Death and decay of cyanobacteria leads to the generation of humus and improvement in the soil structure and fertility (Abdel-Raouf et al. 2012). Microbial biomass inclusive of cyanobacteria acts as labile sink and source of nutrients in the submerged rice field ecosystems (De Datta 1987; Mandal et al. 1998). Therefore, Choudhury and Kennedy (2004) observed that even in the absence of any fertilizer inputs, wetland rice field systems can produce a grain yield of 2–4 t ha^{-1}. Application of the cyanobacterial biofertilizers *Aulosira fertilissima* (12.5 kg ha^{-1}) and urea (90 kg ha^{-1}) significantly increased the biomass and yield of rice (Dubey and Rai 1995). Jha and Prasad (2006) also observed increase in grain and straw yield in rice through the application of cyanobacterial biofertilizers. Kaushik et al. (2019) reported that higher yields can be ensured due to judicious application of nitrogenous fertilizers and cyanobacteria. The production cost involved in rice cultivation reduced by half when the recommended dose of chemical nitrogen was replaced by 50% with cyanobacterial biofertilizers (Chittapun et al. 2018).

Beneficial effects of cyanobacteria on crops that do not require flooded conditions have been reported (Dadhich et al. 1969; Kaushik and Venkataramanan 1979). Therefore, the ambit of cyanobacterial application has now been expanded to crops other than rice (Nain et al. 2010; Manjunath et al. 2011). Application of cyanobacteria *per se* as biofertilizer was found to be beneficial in wheat (Obreht et al. 1993; Gantar et al. 1995a, b). *In vitro* positive results were also found with cyanobacterial inoculation resulting in improvement of the plant shoot/root length, dry weight and yield (Spiller and Gunasekaran 1990; Karthikeyan et al. 2007, 2009). Similarly, their inoculation along with plant growth producing rhizobacteria resulted in the biofortification of wheat (Rana et al. 2012). Cyanobacteria-mediated plant growth promotion was observed in tomato (Prasanna et al. 2013). Recently, Prasanna et al. (2015) developed a formulation based on cyanobacteria for integrated nutrient management in maize crops. Evaluation of the interaction among maize hybrids and cyanobacterial inoculants showed positive influence due to cyanobacterial application (Prasanna et al. 2016). Because of the properties of the cyanobacteria mentioned above, attempts have been made to develop carrier based biofertilizers for effective delivery and physiological stability/effects (Venkataraman 1972; Kaushik 2004; Jha and Prasad 2006; Prasanna et al. 2013).

Maintenance of ion homeostasis is an integral component of the drought and salinity stress management. Ionic adjustments through restricted entry of sodium and its active efflux enhance the salt tolerance in cyanobacteria (Reed et al. 1984b; Apte et al. 1987). Operation of Na^+/H^+ antiporter mechanism helps in the efflux of sodium and maintenance of low intracellular sodium content in cyanobacteria (Elanskaya et al. 2002; Berry et al. 2003; Tsunekawa et al. 2009). Accumulation of potassium ions is required for various cellular processes and the biosynthesis of organic osmolytes is important in salinity and desiccation tolerance of cyanobacteria (Apte and Alahari 1994; Matsuda et al. 2004). Nanatani et al. (2015) observed that in *Synechocystis* PCC 6803, high affinity K^+ uptake system helps in maintaining turgour and K^+/Na^+ ratio. Protection of the cell membrane system and cellular enzymes is important in response to drought and salinity. Several cyanobacteria accumulate low molecular weight organic solutes which are synthesized either *de novo* or accumulated from the medium. Accumulation of compatible solutes such as quarternary ammonium compounds, sugars and glycine betaine lead to osmoprotection in cyanobacteria (Erdmann 1983; Reed and Stewart 1983; Reed et al. 1984a, 1986; Borowitzka 1986; Waditee et al. 2002). Synthesis and accumulation of glucosyl glycerol as compatible solute was reported in the cyanobacterium *Synechocystis* PCC 6803 due to salinity (Hagemann 2011; Kirsch et al. 2019). In cyanobacteria such as *Anabaena* and *Nostoc* sp. synthesis of osmotic stress/water stress proteins conferred osmotic protection and modification of osmotic tolerance (Fulda et al. 1999). Production of reactive oxygen species (ROS) is deleterious to the cells in response to drought and salinity stress. However, increase in the antioxidant activity confers stress tolerance to the cyanobacteria. Increase in the antioxidant defense due to upregulation of level of proline, superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT) and glutathione reductase (GR) in *Anabaena* sp. resulted in enhanced halotolerance (Yadav et al. 2016). Therefore, the salt tolerance mechanism(s) employed by the cyanobacteria is important in their exploitation for the efficient management of drought and salinity stress in crop plants.

Plant growth promoting rhizobacteria and stress alleviation

The zone surrounding the plant root where the soil biological and chemical properties are influenced by the root is known as rhizosphere. Rhizospheric region of the soil is rich in nutrients due to the accumulation of plant/root exudates such as sugars and amino acids which is a source of energy for bacteria (Gray and Smith 2005). Bacteria that colonize the rhizosphere are known as rhizobacteria (Schroth and Hancock 1982). The interaction between rhizosphere and the microbes is considered to be positive, negative or neutral (Pii et al. 2015). Positive effects are observed when bacteria associated with roots are able to induce positive effects on the plant growth and fitness. Pathogenic bacteria producing metabolites with toxic effects can have detrimental effects on plant growth leading to negative interactions. However, in neutral interactions, rhizobacteria can take up the root exudates as nourishment without affecting the growth of plants (Lynch 1990; Dobbelaere et al. 2003). Bacteria belonging to diverse genera which aids in plant growth have been identified as plant growth promoting rhizobacteria (PGPR) and the most predominant being *Pseudomonas*, *Bacillus*, *Enterobacter*, *Penibacillus*, *Arthrobacter* and *Acinetobacter* etc. (Zhang et al. 2017). Plant growth promoting rhizobacteria exert beneficial effects on the growth and development of many crop plants and a number of studies have been conducted to understand the beneficial effects of these rhizobacteria (Wang et al. 2012; Mendes et al. 2013; Willis et al. 2013; Govindasamy et al. 2020). The surface of above-ground organs of plants, especially the phyllosphere is densely populated by bacteria (Remus-Emsermann et al. 2014). Ali et al. (2009) observed that the plant growth promoting compounds produced by phyllospheric bacteria influence the growth and development of host plants. Rhizospheric bacteria capable of altering the physiological response of plants under water stress have been reported (Naylor and Coleman-Derr 2018). Complex microorganisms and microbial communities colonize the plant endosphere (Compant et al. 2021). Certain bacteria found in the plant endosphere stimulate plant growth through the production of hormones and increasing the nutrient availability resulting in resilience to abiotic stresses (Bulgarelli et al. 2013). Thus, the natural associations of microorganisms with plants residing in the phyllosphere, rhizosphere and the endosphere lead to beneficial effects such as production of hormones, increasing the nutrient availability and enhancing the water availability etc. (Oleńska et al. 2020). Root-tissue colonizing bacteria such as *Ochrobactrum* sp. EB-165, *Microbacterium* sp. EB-65, *Enterobacter* sp. EB-14 and *Enterobacter cloacae* strain EB-48 isolated from Sorghum plants showed plant growth promotion as well as induced stress tolerance (Govindasamy et al. 2020).

Bacteria belonging to different phylogenetic groups colonize the intercellular spaces and vascular tissues (Compant et al. 2010; Reinhold-Hurek and Hurek 2011). Such bacteria are known as endophytes and can have beneficial interactions with the plants and contribute significantly to the nutrient supply of their host plant (George et al. 2013). The endophytic bacterial diversity showed richness of the species and helps in the solubilization of phosphate and assimilation of nitrogen (Rosenblueth and Martínez-Romero 2006). On the other hand, in an endosymbiotic bacterial interaction, beneficial endophytic microorganisms are accommodated within a host membrane intracellularly through the development of an organized symbiotic structure and contribute significantly to the nutrient supply of their host plant and can help the plant to overcome a variety of abiotic stresses (Govindasamy et al. 2018).

Plant growth promoting rhizobacteria improve plant growth either directly or indirectly through various mechanisms. Several reports are available on the ability of these organisms to produce signalling molecules known as elicitors. The elicitors can bind to the receptor sites on plasma membrane and trigger signalling cascades leading to activation of genes that produce enzymes and proteins or the secondary metabolites (Nürnberger et al. 1994; Zhao and Sakai 2003a, b, Zhao et al. 2004, 2005). Some of these compounds produced by the plant growth producing rhizobacteria also help the plants to develop tolerance to abiotic stress such as salinity (Dodd and Perez-Alfocea 2012). Rhizobacterial and bacterial endophytes induced physical and chemical changes in plants leading to enhanced tolerance against various abiotic stresses such as drought and salinity has been observed (Dimkpa et al. 2009; Yang et al. 2009). Inoculation of rhizobacteria played a significant role in enhancing osmotic stress tolerance in *Capsicum annuum* (Sziderics et al. 2007). Induced systemic tolerance (IST) through rhizobacteria mediated production of elicitors such as enzymes, volatiles, phytohormones, antioxidants and exopolysaccharides have been reported (Govindasamy et al. 2011). Studies conducted by Sziderics et al. (2007) and Govindasamy et al. (2011) revealed that the application of plant growth promoting rhizobacteria induce tolerance through expression of host plant stress-responsive genes.

As highlighted before, plant growth and productivity are greatly affected by environmental stresses such as drought, high salinity and high/low temperature (Zheng et al. 2010). Therefore, the microorganisms offer an opportunity to mitigate the abiotic stress induced challenges in crop production. Only a few phylogenetic groups of rhizobia and mycorrhizal fungi had their plant beneficial effects targeted under stressed and unstressed environments. Enebe and Babalola (2018) have described the influence of plant growth promoting rhizobacteria in relation to abiotic stress tolerance and plant growth. Induction of induced systemic resistance to drought and salinity by plant growth promoting rhizobacteria was reported (Yang et al. 2009). Willis et al. (2013) highlighted the role of arbuscular mycorrhizal fungi and roots of higher plants in stressed environment. Lugtenberg et al. (2013) observed that inoculation of crop plants with beneficial microbes improved salinity tolerance and yield. A strain of *Pseudomonas fluorescens* isolated from the rhizosphere of the date palm from the desert region promoted root growth in Maize seedlings under salinity stress (Zerrouk et al. 2016). It was observed that the halophilic bacterium, *Serratia* sp. Sl-12 isolated from a salt lake improved salinity tolerance and increased the shoot biomass in wheat (Singh and Jha 2016). Thus, the application of PGPR inoculants in the agricultural fields was found to be a promising strategy to combat salinity and increase food production (Ilangumaran and Smith 2017).

Possibility of employing cyanobacteria for the management of abiotic stress in crop plants

The role of cyanobacteria in the management of abiotic stress is gaining importance. In this context, various mechanisms such as production of hormones, amino acids, vitamins, exopolysaccharides, compatible solutes and antioxidants would be important in cyanobacteria mediated drought and salinity stress tolerance in plants. Furthermore, the potential of nitrogen fixation and the ability to regulate the ion metabolism is also important in efficient stress management. The mechanisms operating in cyanobacteria and their possible role in alleviation of drought and salinity stress are important for further exploiting them in sustainable agriculture.

Drought

Diminishing availability of water poses a threat to the proliferation of cyanobacteria and in the fields, they are constantly exposed to continuous dehydration, desiccation and re-wetting. Drought tolerant cyanobacteria can be used as biofertilizer for crops such as wheat, sugar cane, cotton, sorghum, and vegetables (Abd-Alla et al. 1994). Reports are available on the desiccation tolerance of a number of cyanobacteria (Potts 1994). Cyanobacteria exhibit considerable resilience to osmotic/water stress due to their ability to regulate ion fluxes, accumulation of compatible solutes and through the expression of tolerant genes and protein synthesis (Borowitzka 1986; Fernandes et al. 1993; Apte 2001). However, it has also been observed that vital metabolic activities of cyanobacteria such as photosynthesis, respiration and nitrogen fixation revive within minutes of re-wetting (Sherer et al. 1984). In the cyanobacterium *Anabaena* PCC 7120, the genes involved in photosynthesis, nitrogen metabolism and protein synthesis are down-regulated during dehydration (Katoh et al. 2004). On the other hand, a remarkable capacity to repair the highly disintegrated genome and proteome was also observed in response to desiccation (Singh et al. 2013). The role of cyanobacteria is important in relation to plant growth and nutrient management under drought stress conditions. It was observed that the production of exopolysaccharides by cyanobacteria helps in enhanced retention of water, nutrients and ensure the survival of microorganisms from desiccation and nutrient limitation (Zhang 2005; Colica et al. 2014; Adessi et al. 2018). Stress priming is an adaptive strategy to enhance the stress tolerance of plants. Priming of the seeds of *Senna notabilis* and *Acacia hilliana* with cyanobacterial strains *Nostoc* sp. and *Microcoleus* sp. resulted in better germination and establishment of the plants in drought affected ecosystem (Muñoz-Rojas et al. 2018b). Chua et al. (2019) reported that bio-priming of the seeds with different cyanobacterial strains improved growth of *Eucalyptus gamophylla* and *Grevillea wickhamii* plants used in the restoration of drylands.

Biological soil crusts or biocrusts are commonly found in dry lands and it consists of several microorganisms in varying proportions (Maestre et al. 2011). These biocrusts are often found at the top soil of the terrestrial ecosystem. Lin and Wu (2014) observed that the biological soil crusts are dominated by cyanobacteria. In biocrusts, the cyanobacteria are pioneer organisms among biological communities that improve soil conditions and promote the colonization and succession of other species such as lichens and mosses (Belnap and Gardner 1993; Lan et al. 2013). Further, it has been observed that the biological crusts ensure soil water availability (Chamizo et al. 2016), soil stability (Rodríguez-Caballero et al. 2012) and nutrient cycling (Delgado-Baquerizo et al. 2013). Recently, cyanobacteria have been employed to develop biological soil crusts even under laboratory conditions (Park et al. 2017). Chamizo et al. (2018) also observed that the formation of biocrusts improves stability and fertility of different soils due to inoculation with nitrogen fixing and non-nitrogen fixing cyanobacterial species. The cyanobacterium *Leptolyngbya ohadi* found in the biocrust produces complex exopolysaccharides that maintain hydration, chelates nutrients and aggregates sand (Mugnai et al. 2018b). Muñoz-Rojas et al. (2018a) demonstrated the capability of cyanobacteria in the formation of biocrust and substantial increase in the total organic carbon content of the soil. Becerra-Absalón et al. (2019) reported that the common cyanobacterial strains found in the biocrusts of dry lands of Central Mexico consists of species of *Scytonema hyalinum*, *Scytonema crispum*, *Nostoc* sp., *N. commune* and *Calothrix parietina*. All these studies have showed the potential of cyanobacteria to survive and grow in extremely desiccated conditions. Therefore, the drought tolerant cyanobacterial strains can be employed to develop strategies for the management of drought stress. However, very little information is available regarding the cyanobacteria mediated enhancement in growth of plants from extreme environmental conditions such as drought.

Salinity

Increase in the salinity level of the soil leads to changes in the water potential and osmotic equilibrium and create “physiological dryness” in the cells. However, the cyanobacteria exhibit considerable salinity tolerance and have been found to grow in salt affected soils (Thomas and Apte 1984). Reports are available on the reclamation of salt affected soils using cyanobacteria (Roman et al. 2018). It was observed that the cyanobacteria form a thick stratum on the soil surface and conserve the organic C, N and P as well as moisture and convert the Na^+ clay to Ca^{2+} clay and hence they are considered ideal candidates for the reclamation of usar soils which are impermeable and unproductive due to the presence of undesirable salts (Singh 1961). Significant level of salinity tolerance in the range of 7 to 15 g L^{-1} was observed in species such as *Anabaena oscillarioides*, *Anabaena aphanizomenoides* and *Microcystis aeruginosa* (Coutinho and Seeliger 1984; Moisander et al. 2002). Salinity tolerance in many cyanobacteria can be due to the operation of different types of Na^+/H^+ antiporters that play a key role in maintaining low sodium concentrations in the cell (Waditee et al. 2002; Wutipraditkul et al. 2005) or even, to increase the photosynthetic activity and the accumulation of compatible solutes (Joset et al. 1996; Hagemann 2011).

Inoculation of cyanobacteria was found to be beneficial in providing abiotic stress tolerance in various crop plants (Table 2). *Anabaena torulosa*, a brackish-water nitrogen-fixing cyanobacterium grew successfully and fixes nitrogen on moderately saline “Kharland” soils (Apte and Thomas 1997). de Caire et al. (1997) observed considerable enhancement in soluble carbon and aggregation of soils inoculated with *N. muscorum*. In rice seedlings, most of the salinity induced effects on growth and biochemical alterations were either partially or completely reversed by the extracellular products secreted by *Scytonema hofmanni* (Rodríguez et al. 2006). Cyanobacterial inoculation in rice plants stressed with heavy metals improved the growth and yield due to improvement in the mineral nutrition and reduction in metal uptake (Tripathi et al. 2008). Application of cyanobacteria not only enhanced the soil biomass but also reduced the soil salinity and suppressed the weed growth in paddy fields (Saadatnia and Riahi 2009). Singh and Singh (2015) employed the halotolerant cyanobacterium *Nostoc calcicola* in combination with gypsum and observed it as a better option to reclaim saline-alkaline soils. To reclaim the salt affected soils, various strategies have been used which involve chemical, physical and biological methods (Luo et al. 2018; Saifullah et al. 2018; Zhao et al. 2018). Apte and Thomas (1997) identified the potential of *Anabaena torulosa* in reducing the electrical conductivity (EC) of highly saline soil. Nisha et al. (2018) observed that inoculation of cyanobacteria such as *Nostoc ellipsosporum* HH205 and *Nostoc punctiforme* HH-206 improved the physico-chemical and biological properties of the soil besides promoting the yield of pearl millet and wheat. They have attributed the improvement in the organic carbon, nitrogen and other nutrients in the soil due to the autotrophic nature and nitrogen fixing potential of cyanobacteria. Furthermore, the application of cyanobacteria decreased the bulk density and enhanced the water holding capacity of the soil. Roman et al. (2018) observed that the properties of sodic soils were improved through the application of cyanobacteria such as *N. commune*, *Scytonema hyalinum* and *Tolypothrix distorta*. The results obtained from these studies are important in the exploitation and field application of cyanobacteria for the remediation of salt affected soils. Further, it was suggested that restoration of soil fertility and removal of salts could be achieved using combinations of salinity tolerant plants and cyanobacteria (Jesus et al. 2015). Sustained nitrogen fixation will be maintained under saline growth conditions by the application of cyanobacteria. However, the prevailing soil conditions in the stressed environments may lead to reduction in the potential of biological nitrogen fixation (Dash et al. 2018). Wang et al. (2015) observed that cyanobacterial biological nitrogen fixation is critical for the remediation of salt affected soils.

Biological methods involving cyanobacteria as potential candidates have been employed in the bioremediation of salt-affected soils (Rady et al. 2018; Roman et al. 2018). Rice plants were grown on salt stressed soil (pH

Table 2 Applications of cyanobacteria and the mechanisms imparting abiotic stress tolerance in different crops

Cyanobacteria	Crop	Type of abiotic stresses	Role in relation to to abiotic stress tolerance	References
Nostoc carneum TUBT04 and *N. carneum* TUBT05	Rice	Salinity	Enhancement in growth and yield	Chittapun et al. (2018)
Anabaena oryzae, *Anabaena doliolum*, *Phormidium fragile*, *Calothrix geitonos*, *Hapalosiphonin tricatus, Aulosira fertilissima*, *Tolypothrix tenuis*, *Oscillatoria acuta* and *Plectonema boryanum*	Rice	Salinity	Enhanced accumulation of phytohormones and plant growth promotion	Singh et al. (2011)
Nostoc sp., *Anabaena doliolum*, *Calothrix* sp., *Westiellopsis* sp. and *Phormidium papyraceum*	Rice	Heavy metal	Improvement in growth, yield and mineral composition of the plants	Tripathi et al. (2008)
Nostoc muscorum	*Trigonella foenumgracum*	Heavy metal	Improvement in seed sugar, protein and lipid content	Mohsen et al. (2013)
Nostoc commune	*Brassica* sp.; *Capsicum* sp.; *Lactuca* sp.; *Allium* sp.	Radio-isotope	Promotion of early germination and high rooting	Katoh et al. (2012)
Nostoc sp. and *Microcoleus* sp.	*Senna notabilis* and *Acacia hilliana*	Drought	Priming of the seeds resulted in their better germination and establishment	Muñoz-Rojas et al. (2018a)
Nostoc kihlmani and *Anabaena cylindrica*	Wheat	Salinity	Improvement in structure of the soils and wheat growth	Gheda and Ahmed (2015)
Nostoc calcicola, *Nostoc spongiaeformae*, *Nostoc linckia* and *Nostoc muscorum*	Wheat, Maize and Rice	Salinity	Enhancement in seed germination, vigour index and mobilization efficiency	Arora et al. (2010)
Leptolyngbya sp., *Microcoleus* sp., *Nostoc* sp. and *Scytonema* sp.	*Eucalyptus gamophylla* and *Grevillea wickhamii*	Drought	Bio-priming of the seeds with the cyanobacteria showed positive results on radicle initiation, shoot and root growth	Chua et al. (2019)
Anabaena vaginicola ISB42, *Nostoc calcicola* ISB43, *Trichormus ellipsosporus* I SB44 and *Cylindrospermum michailovskoense* ISB45	*Mentha piperita*	Salinity	Increases in plant growth and oil content	Shariatmadari et al. (2015)

8.8, EC 5.2 dS/m) and inoculated with different strains of cyanobacteria namely *Anabaena oryzae*, *Anabaena doliolum*, *Tolypothrix tenuis*, *Aulosira fertilissima*, *Calothrix geitonos*, *Plectonema boryanum*, *Phormidium fragile* and *Oscillatoria acuta* (Singh et al. 2011). Inoculation of cyanobacteria has resulted in significant enhancement in the accumulation of phytohormones and plant growth promotion. Significant enhancement in seed germination, vigour index and nutrient mobilization efficiency was observed in rice, wheat and maize plants subjected to salinity stress and inoculated with cyanobacteria (Arora et al. 2010). Chittapun et al. (2018) also showed improvement in growth and yield in salinity stressed rice plants inoculated with cyanobacteria. Improvement in the structural characteristics and growth was observed in wheat plants due to cyanobacterial application under salinity stress conditions (Gheda and Ahmed 2015). Shariatmadari et al. (2015) observed that application of cyanobacteria in *Mentha piperita* exposed to salinity stress enhanced plant growth and oil content. Thus, the salinity tolerant cyanobacteria could be exploited for plant growth promotion under salt stressed environments. Evaluation of salt tolerant strains under pot experimentation and field based trials is therefore critical for their exploitation in the management of salinity stress.

Conclusions and Future perspectives

Food security is directly related to agriculture, which is a highly vulnerable sector to climate change. Drought and salinity stress conditions restrict crop growth and yield and therefore optimal growth of plants is not possible in such stressed environments. Soil health is important in the sustenance of agriculture, but climate change induced drought, salinity and other accelerated edaphic stressors pose a serious threat to the agriculture. Microbe based interventions for the reclamation of salt and drought affected soil is an important strategy in maintaining the agricultural sustainability. In the soil, large populations of microbes exist, which form a dynamic and complex ecological community and these microbial populations influence the plant growth, development and productivity through their synergistic interaction. The roots maintain its associated beneficial microbiome which can influence the plant traits positively. Such associations are further important due to their ability to promote plant growth especially under drought and salinity stress conditions. One of the most important constituents of soil microbial community is the cyanobacteria. It has been observed that inoculation of cyanobacteria improved the soil properties, microbial community dynamics that leads to further availability and uptake of nutrients by plants. Several cyanobacteria produce extracellular polysaccharides which play an important role in withholding of salt and water and help in the improvement of soil nutrient dynamics. Inoculation of cyanobacteria in the rhizosphere of drought/salinity stressed ecosystem may lead to enhancement in various soil properties and trigger plant growth through various direct and indirect mechanisms as illustrated in Fig. 1. The cyanobacteria can help plants from the adverse consequences of the stress through a range of mechanisms such as nitrogen fixation, improved microbial biomass, mobilization of nutrients, induced systemic tolerance, production of phytohormones, exopolysaccharides. vitamins, peptides, antioxidants and osmolytes. Apart from improving the soil structure, the exopolysaccharides also protect the cyanobacteria from adverse conditions and help them to survive under drought and salinity. Cyanobacteria can therefore play an important role in improving plant adaptation to drought and salinity stress. Hence, the application of cyanobacteria in the management of drought and salinity stress is gaining considerable importance. However, systematic efforts have not been undertaken to assess their drought and salinity tolerance imparting potential. In this context, it is important to isolate, screen and identify drought and salinity tolerant cyanobacterial strains from drought and salinity affected areas as potential inoculants. Several difficulties and constraints have been encountered in the mass multiplication of cyanobacteria, like poor growth and contamination during their large scale multiplication is a matter of concern which needs to be addressed. In the absence of proper delivery mechanisms, it will be difficult to enhance their field efficacy. Therefore, proper delivery mechanisms using appropriate carrier may be developed to improve the viability and efficacy of cyanobacteria based bioinoculants. Based on the information already available, the research focus must be directed towards the identification and evaluation of potential cyanobacterial strains for plant growth promotion attributes under abiotic stress environments. Besides, a detailed understanding of induced systemic tolerance mechanisms by cyanobacteria against abiotic stress factors will further drive their utility and application in agriculture to enhance the survival of plants under drought and salinity stress. Therefore, development of efficient formulations based on cyanobacteria is important in improving the soil health and plant growth in stressed environments.

Agricultural productivity is adversely affected by increasing incidences of drought and salinity stress. Cyanobacteria play an important role in plant growth promotion and furthermore the cyanobacteria found in drought and salt affected soils exhibit considerable stress tolerance and display plant growth promoting attributes. Therefore, the progress made in cyanobacterial research on the physiological, biochemical, and molecular aspects of drought and salinity

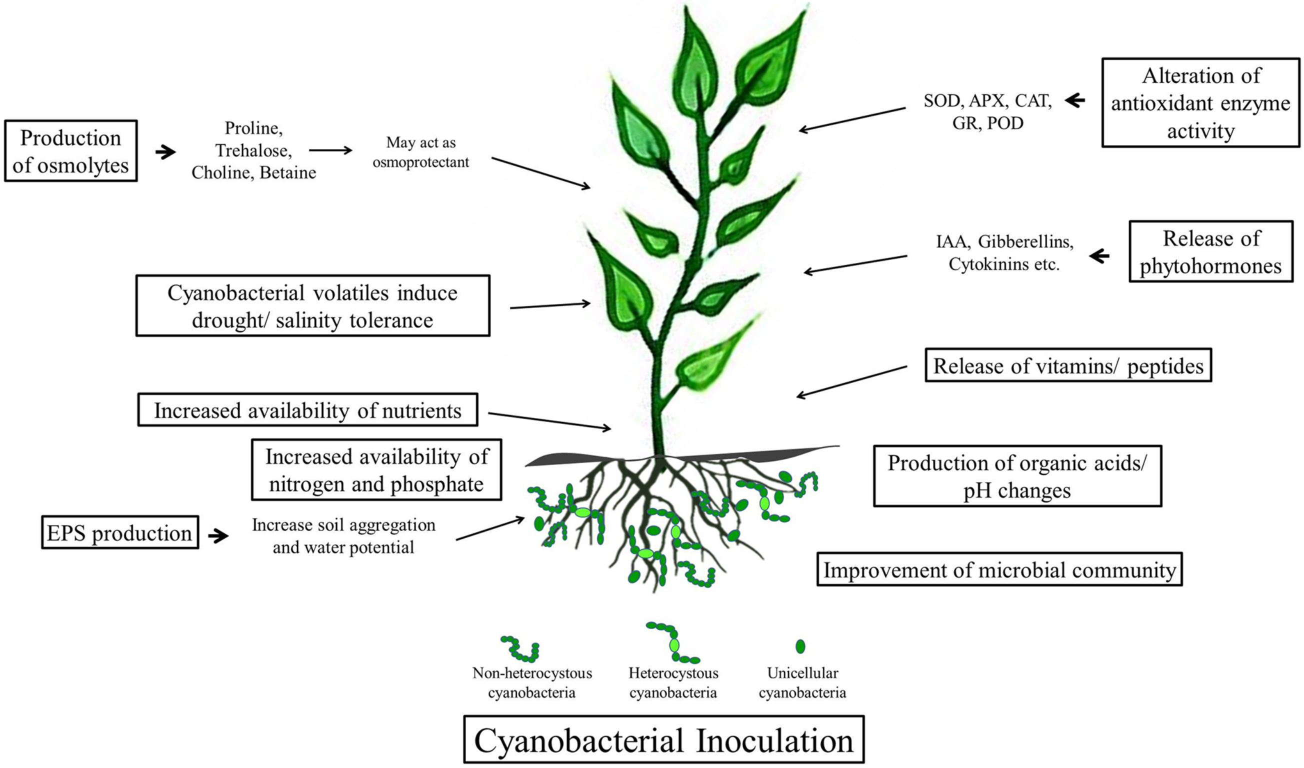

Fig. 1 Mechanism of salinity/drought tolerance in plants induced by cyanobacteria

tolerance will have broader applications in selecting potential strains for the mitigation of stress and management. Characterization of drought and salinity tolerant cyanobacteria is thus important in the mitigation and protection of plants from these stresses. However, their effectiveness will be further significant if they also exhibit multiple plant growth promoting traits such as phosphate solubilization, nitrogen fixation, indole acetic acid production, and siderophore production etc. Cyanobacteria mediated alleviation of drought and salinity stress in plants needs further research and field trials.

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Declarations

Conflict of interest The authors declare no competing interests.

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