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Role of Plant Growth-Promoting Rhizobacteria (PGPR) in the Improvement of Vegetable Crop Production Under Stress Conditions

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Abstract

Biotic and abiotic stresses are major constrains to agricultural production. Among abiotic stress, drought and salinity are the major environmental factors limiting growth and productivity of many crops including vegetables, particularly in arid and semiarid areas of the world. Abiotic stress causes more than 50% average yield loss worldwide. Globally, demand for vegetables is increasing, and this has boosted the vegetable production in recent times. The substantial increase in production of key vegetables such as tomato, onion, cucumber, eggplant, cauliflower, pepper, lettuce, carrot, and spinach has been recorded. However, vegetables are generally considered more vulnerable than staple crops to stressful environmental conditions including extremes of temperature, drought, salinity, water logging, mineral nutrient excess and deficiency, and changes in soil pH which are likely to be exacerbated by the prevalent climatic change in many parts of the world. Plant growth under stress conditions on the contrary may be enhanced by the application of microbial inoculation including plant growth-promoting rhizobacteria (PGPR). These microbes promote plant growth by regulating nutritional and hormonal balance, producing plant growth regulators, solubilizing nutrients, and inducing resistance against plant pathogens. In addition to their interactions with plants, these microbes exhibit synergistic as well as antagonistic interactions with other soil microbiota. These interactions are vital to maintain soil fertility and concurrently the growth and development

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of vegetables under stress conditions. The present literature comprehensively discusses recent developments on the effectiveness of PGPR in enhancing vegetable growth under stressful environments.

4.1 Introduction

Population of the world is predicted to increase beyond 8 billion by 2030 which is likely to pose major challenges for agricultural sector to secure food availability (Smol 2012). In the developing countries, abiotic stresses such as soil salinization, soil sodification, drought, soil pH, and environmental temperature are major limiting factors in crop production. Of these, soil salinization and drought are the two major factors endangering the potential use of soils and leading to soil degradation and soil desertification (Ladeiro 2012). The Global Assessment of Soil Degradation (GLASOD) estimated that about 13% (or 850 million ha) of the land in Asia and the Pacific is degraded due to soil salinization, soil sodification, and drought (Ladeiro 2012). Abiotic stress is the primary cause of worldwide crop loss, leading to more than 50% crop yield reduction (Shahbaz and Ashraf 2013). Plants as sessile organisms are constantly exposed to changes in environmental conditions; when these changes are rapid and extreme, plants generally perceive them as “stress” (Carillo et al. 2011). Drought and salinity are the two most devastating environmental stress, which is increasing day by day and reducing the agricultural productivity in large areas of the world (Hasanuzzaman et al. 2013). According to the United States Department of Agriculture (USDA), onions are highly sensitive to saline soils, while cucumbers, eggplants, peppers, and tomatoes are sensitive to salinity (Nandakumar et al. 2012). The majority of horticultural and cereal crops cultivated are susceptible to excessive concentrations of dissolved ions (30 mM or 3.0 dS/m) in the rhizosphere (Ondrasek et al. 2010). Horneck et al. (2007) have reported 50% yield reduction in potato, corn, onion, and bean when soil EC is increased to 5 dS/m. Sibomana et al. (2013) reported 69% tomato yield reduction due to water stress. Also, many studies have shown that salinity reduces microbial activity and microbial biomass and changes microbial community structure (Andronov et al. 2012). On the other hand, soil water content controls microbial activity and is a major factor that determines the rates of mineralization (Paul et al. 2003).

To minimize crop loss, scientists have attempted to develop salt-tolerant crop through breeding (Araus et al. 2008; Witcombe et al. 2008). However, gaps in understanding the complex physiological, biochemical, developmental, and genetic basis of environmental stress tolerance, and the subsequent difficulty in combining favorable alleles to create improved high yielding genotypes, are the major constraint to improve crop yield under abiotic stress (Dwivedi et al. 2010). Apart from the development of some salt-tolerant plant species, a wide range of salt-tolerant plant growth-promoting rhizobacteria such as *Rhizobium*, *Azospirillum*, *Pseudomonas*, *Flavobacterium*, *Arthrobacter*, and *Bacillus* have also shown beneficial interactions with plants in stressed environments (Egamberdieva 2011).

Here, an attempt is made to overview the effects of drought and salinity on crop plants especially vegetables and to identify/develop management strategies to overcome such effects on vegetables grown distinctly in different agroecological regions.

4.2 Stress Factors

4.2.1 Soil Salinization

Soil in which the electrical conductivity (EC) of the saturation extract (ECe) in the root zone exceeds 4 dS/m (approximately 40 mM NaCl) at 25 °C and has exchangeable sodium of 15% is referred to as salinity in soil (Jamil et al. 2011). Agricultural losses caused by salinity are difficult to assess, but these have been estimated to be substantial and expected to increase with time. It has been estimated that 20% of the total cultivated and 33% of the irrigated agricultural lands are affected by high salinity (Shrivastava and Kumar 2015). Annually salinized areas are increasing at a rate of 10% due to various reasons such as high surface evaporation, low precipitation, saline water irrigation, and poor cultural practices, and it has been estimated that >50% of the cultivatable land would be salinized by 2050 (Jamil et al. 2011). Soil salinity can also be a consequence of natural causes, such as (1) weathering of parent rocks and minerals in the soil, which releases various ions (e.g., Na, Ca, K and Mg, sulfates, and carbonates) to the soil solution (Moreira-Nordemann 1984); (2) seawater intrusion into coastal areas leading to increased salinity levels in the soil and channel water, which may be the major factor causing reduction in crop production (Kotera et al. 2008; Mahajan and Tuteja 2005); (3) rainwater containing 50 mg/l NaCl (Munns and Tester 2008) which can result in the precipitation of 250 kg NaCl per ha for every 500 mm of annual rainfall; and (4) wind-borne materials from lake or land surfaces. Nevertheless, the more significant proportion of saline soils is attributed to intensive agricultural cultivation (FAO 2008). The removal of natural perennial vegetation and its replacement with annual agricultural crops was perhaps the first factor in man-induced salinity (Manchanda and Garg 2008). Use of salt-rich irrigation water is undoubtedly one of the foremost factors responsible for soil salinity. In addition, improper irrigation management, which might be responsible for rise in the water table, known as secondary salinization, is an important contributor to soil salinity. Based on the salinity development, salt-affected soils can be classified into (1) primary salinity, which occurs naturally where the soil parent material is rich in soluble salts or geochemical processes resulting in salt-affected soil, and (2) secondary salinity, salinization of land and water resources due to human activities. Human activities like poor irrigation management, insufficient drainage, improper cropping patterns and rotations, and chemical contamination can also induce salinization.

In India, approximately 7 million hectares of land is covered by saline soil (Patel et al. 2011), most of which occurs in Indo-Gangetic Plain that covers the states of Punjab, Haryana, Uttar Pradesh, Bihar, and some parts of Rajasthan. Arid tracts of Gujarat and Rajasthan and semiarid tracts of Gujarat, Madhya Pradesh, Maharashtra,

Table 4.1 Degree of salinity in soil and plant response

Degree of salinity	Electrical conductivity (dS/m)	Level of effect	Use	Plant response	Salt-tolerant crops
Nonsaline	0–2	Salinity effects are negligible	Cropping	Very little effect on plant	Carrot Okra Radish
Low salinity	2–4	Salinity effects are minimal	Cropping	Yields of sensitive crops may be restricted	Celery Common beans Pea
Moderate salinity	4–8	Yield of the plant is restricted	Crop-pasture rotation	Some effect on salt-sensitive crops	Cabbage Tomato Potato Onion Peas Squash Cucumber Cauliflower Eggplant
High salinity	8–16	Only salt-tolerant plants yield satisfactory	Grazing or revegetation	Considerable effect on salt-sensitive crops	Artichoke Beetroot
Very high salinity	<16	Few salt-tolerant plants yield satisfactory	Very few plants will tolerate and grow	Some effect on salt-tolerant crops	Asparagus

Adapted from Abou-Baker and El-Dardiry (2015)

Karnataka, and Andhra Pradesh are also largely affected by saline lands (Shrivastava and Kumar 2015). When salt accumulates in soil, excessive sodium from salt destroys soil structure and hydraulic properties of soil, increases soil pH, and reduces infiltration of water and aeration in soil leading to soil compaction, soil erosion, and water runoff (Ondrasek et al. 2010). Further, sodium is the most pronounced destructor of secondary clay minerals by dispersion. Dispersed clay particles undergo leaching through the soil and may accumulate and block pores, especially in fine-textured soil horizons (Burrow et al. 2002). The soil becomes unsuitable for proper root growth and plant development (Table 4.1).

Saline soil inhibits plant growth, firstly by reducing the ability of the plant to take up water which in turn reduces the growth rate. This is referred to as “osmotic or water-deficit effect of salinity.” Secondly, if excessive amounts of salt enter the plant in the “transpiration stream,” there will be injury to cells in the transpiring leaves. This is called the “salt-specific or ion-excess effect of salinity” (Greenway and Munns 1980). Salinity is often caused by rising water tables, and it can be accompanied by water logging. Water logging itself inhibits plant growth and also reduces the ability of the roots to exclude salt, thus increasing the uptake rate of salt and its accumulation in shoots.

4.2.1.1 Effect of Salinity on Plant Growth

Most of the widely used crops in human or animal nutrition such as cereals (rice, maize), forages (clover), or horticultural crops (potatoes, tomatoes) require extensive irrigation practices, but are also susceptible to excessive concentration of salts either dissolved in irrigation water or already present naturally in soil (rhizosphere) (Ondrasek et al. 2010). When present in excess, salts cause osmotic and ionic stress such as toxicity of Na^+ in plants. These stresses result in complete or partial stomata closure, C assimilation reduction, reduced leaf area and chlorophyll content, accelerated defoliation (Shannon and Grieve 1999), nutritional imbalance (reduced intake N, Ca, K, P, Fe, Zn), alteration of metabolic processes, membrane disorganization, reduction of cell division and expansion, and genotoxicity (Carillo et al. 2011). Salt stress like other abiotic stress also leads to oxidative stress due to increased production of reactive oxygen species (ROS), such as singlet oxygen, superoxide anion, hydrogen peroxide, and hydroxyl radical. These ROS are highly reactive and can alter normal cellular metabolism with oxidative damage to carbohydrates, proteins, and nucleic acids and cause peroxidation of membrane lipids (Azevedo Neto et al. 2008). Soil salinity significantly reduces plant phosphorus (P) uptake because phosphate ions precipitate with Ca ions (Bano and Fatima 2009). Together, these effects reduce plant growth, development, and survival. Salinity adversely affects reproductive development by inhabiting microsporogenesis and stamen filament elongation, enhancing programmed cell death in some tissue types, ovule abortion, and senescence of fertilized embryos (Shrivastava and Kumar 2015). In the rhizosphere, excess sodium and more importantly chloride competitively interacts with other nutrient ions (K^+, NO^{3-}, and $H_2PO_4^-$) for binding sites and transport proteins (Tester and Davenport 2003). Uptake and accumulation of Cl^- inhibit nitrate reductase activity, thereby disrupting photosynthetic function (Xu et al. 2000). Once the capacity of cells to store salts is exhausted, salts build up in the intercellular space leading to cell dehydration and death. Salinity has an adverse effect on cell cycle and differentiation. Salinity arrests the cell cycle by reducing the expression and activity of cyclins and cyclin-dependent kinases that result in fewer cells in the meristem, thus limiting growth (Javid et al. 2011).

In a study on vegetables, Bojovic et al. (2010) reported that seed germination of cabbage (*Brassica oleracea*), tomato (*Solanum lycopersicum*), and bell pepper (*Capsicum annuum*) was inhibited at higher concentrations (400–800 Mm) of NaCl. Similarly, Ramazani et al. (2009) and Asaadi (2009) reported decrease in seed germination of fenugreek (*Trigonella foenum-graecum*) due to salinity-induced disturbance of metabolic process leading to increase in phenolic compounds. On the contrary, salinity significant reduction in the leaf area, total root dry weight, photosynthesis, and stomatal conductance of sugar beet was reported by Dadkhah (2011), while Taffouo et al. (2010) confirmed the inhibitory effect of salinity on photosynthesis and photosynthetic pigments in cowpea. A similar study reported an inverse relationship between salt concentration and chlorophylls “a” and “b,” and total chlorophyll content is reported for bean plant (Qados 2011). Kapoor and Srivastava (2010) demonstrated decrease in protein content in black gram plants treated with different salt concentrations. Takagi et al. (2009) reported decreased whole plant biomass with reduced leaf photosynthesis and transport of carbon assimilates as an effect of salinity (100 mM NaCl) in *S. lycopersicum*. Egamberdieva (2011) observed that increasing salt content reduced the shoot length (50%) and root length (7%) of bean seedling grown in a gnotobiotic sand system. Adolf et al. (2013) showed relatively low stomatal conductance (67%) in salt-treated *Titicaca* plant. Several studies have reported reduced nitrogen absorption and accumulation in plants under saline conditions (Silvera et al. 2001). In eggplant, accumulation of Cl^- in leaves was accompanied with decreased concentration of NO_3^- (Savvas and Lenz 2000).

4.2.1.2 Impact of Salinity on Microorganisms

Even though soil microorganisms constitute less than 0.5% (w/w) of the soil mass, they play a key role in maintaining soil fertility (Tate 2000). Microbial biomass is an important labile fraction of the soil organic matter which participates in oxidation, nitrification, ammonification, nitrogen fixation, and other processes which lead to decomposition of soil organic matter and hence to the transformation of nutrients. They can also store C and other nutrients in their biomass which are mineralized after cell death by surviving microbes (Anderson and Domsch 1980). Stress factors are detrimental for beneficial soil microorganisms and have been reported to adversely affect the activity of surviving cells (Chowdhury et al. 2011). Soluble salts in the soil increase the osmotic potential, drawing water out of microbial cells. Low osmotic potential also makes it more difficult for roots and microbes to remove water from the soil (Oren 1999). Soil microbes, however, can adapt to low osmotic potential by accumulating osmolytes. High bioenergetic taxation to maintain osmotic equilibrium between the cytoplasm and the surrounding medium, excluding sodium ions from inside the cell, leads to reduction in growth and activity of the surviving microbes (Chowdhury et al. 2011; Ibekwe et al. 2010). The presence of loose, flexible surface appendage surrounding the bacteria under low electrolyte concentration condition acts as a protective barrier, thereby attenuating the impact of changes in extracellular ionic strength and lowering the osmotic pressure constraint (Francius et al. 2011). With an increase in the salinity level above 5%, the total count of bacteria and *Actinobacteria* were drastically reduced in a study conducted by Wichern et al. (2006). Azam and Ifzal (2006) reported nitrogen immobilization (remineralization and nitrification) process retardation in the presence of NaCl. Soil salinity also inhibits the enzyme activities of benzoyl argininamide, alkaline phosphatase, β-glucosidase, amylase, invertase, catalase, phosphatase, urease, and also microbial respiration (Ghollaratta and Raiesi 2007). A study by Nelson and Mele (2007) concluded a significant decrease in diversity and species richness in rhizosphere microbial community structure indirectly through root exudates quantity and/or quality rather than directly through microbial toxicity as an effect of salinity. Soil salinity has also been reported to disturb the symbiotic interaction between legumes and rhizobia. Singleton and Bohlool (1984) and Rabie et al. (2005) reported decrease in nodulation and nitrogen fixation with reduced nitrogenase activity in legumes such as soybean, common bean, and faba bean.

4.3 Drought

A shortfall in precipitation coupled with high evapotranspiration demand leads to agricultural drought (Mishra and Cherkauer 2010). Drought severity, however, depends on many factors, namely, (1) occurrence and distribution of rainfall, (2) evaporative demands, and (3) moisture storing capacity of soils (Wery et al. 1994). Three main mechanisms which reduce crop yield by soil water deficit are (1) reduced canopy absorption of photosynthetically active radiation, (2) decreased radiation use efficiency, and (3) reduced harvest index (Earl and Davis 2003).

4.3.1 Influence of Drought Stress on Morphological Characteristics of Plants

The effects of drought range from morphological to molecular levels and are evident at all phenological stages of plant growth. Under water stress conditions, which are related to water depletion and/or high atmospheric vapor pressure deficit, photosynthesis decreases through several mechanisms including stomata closure, reduced mesophyll conductance to CO_2, and feedback regulation by end-product accumulation (Nikinmaa et al. 2013). In response to a water deficit stress, ion and water transport systems across membranes function to control turgor pressure changes in guard cells and stimulate stomatal closure (Osakabe et al. 2014). The physiological, biochemical, and molecular responses of plants to drought stress are presented in Table 4.2.

Drought stress impairs mitosis, cell elongation, and expansion resulting in reduced plant height, leaf area, and crop growth (Hussain et al. 2008). Moisture stress during early reproductive growth phase usually reduces yield by reducing the

Table 4.2 Physiological, biochemical, and molecular response of plants to drought stress

Drought stress		
Physiological responses	Biochemical responses	Molecular responses
Recognition of root signal	Transient decrease in photochemical efficiency	Stress-responsive gene expression
Loss of turgor and osmotic adjustment	Decreased efficiency of Rubisco	Increased expression in ABA biosynthetic genes
Decrease in stomatal conductance to CO_2	Accumulation of stress metabolites like MDHA, glutathione, proline, glycine betaine polyamines, and α-tocopherol	Expression of ABA responsive genes
Reduced internal CO_2 concentration	Increase in antioxidants	Synthesis of specific proteins like late embryogenesis abundant
Decline in net photosynthesis	Reduced ROS accumulation	Desiccation stress protein, dehydrins, etc.
Reduced growth rates		

Adapted from Reddy et al. (2004)

Table 4.3 Drought stress and its impact on vegetable crops

Vegetable crops	Critical period of watering	Water stress impact
Brinjal	Flowering and fruit development	Reduced seed viability and yield
Cauliflower, cabbage, and broccoli	Head formation and enlargement	Browning and buttoning in cauliflower
Onion	Bulb formation and enlargement	Splitting and doubling of bulb
Carrot, radish, and turnip	Root enlargement	Distorted, rough, and poor growth of roots
Tomato	Early flowering, fruit set, and enlargement	Flower shedding, lack of fertilization, reduced fruit size, fruit splitting, puffiness
Asparagus	Spear production	Reduce spear quality and increased fiber content
Leafy vegetables	Growth and development of the plant	Toughness of leaves, poor foliage growth
Vegetable pea	Flowering and pod filling	Reduction in root nodulation and plant growth, poor pod filling, poor seed viability
Sweet potato	Root enlargement	Reduced root enlargement with poor yield, growth crack
Sweet corn	Silking, tasseling, and ear development	Crop may tassel and shed pollen before silks on ears are ready for pollination; lack of pollination may result in missing rows of kernels, reduced yields, and poor seed viability or even eliminate ear production

Adapted from Bahadur et al. (2011) and Kumar et al. (2012)

number of fruits/seeds in vegetables, while during flowering and fruit-setting stage, drought stress reduces fruit quality, number of fruits, size of fruits, and finally yield loss (Chatterjee and Solankey 2015). Water stress, mostly at critical period of growth, may drastically reduce productivity and quality of vegetables (Table 4.3).

In a study conducted by Okcu et al. (2005), drought stress impaired the germination and early seedling growth of five pea cultivars tested, while stem length of potato and okra was significantly affected under water stress (Sankar et al. 2008). In a similar study, water stress decreased the growth, total plant dry weight, leaf water potential, leaf relative water content, and leaf pigment of *C. annuum*, whereas contents of malondialdehyde, proline, superoxide dismutase, and peroxidize activity were increased (Qiu-shi et al. 2009).

4.4 Alleviation of Drought and Salinity Stress by Plant Growth-Promoting Rhizobacteria

Abiotic factors and stress have always played a major role in reducing agricultural crop yield. However, to circumvent these effects, scientists have developed several strategies to produce stress-tolerant crops which involve plant breeding and plant genetic engineering, but little success has been achieved so far due to genetic and physiological complexity of the stress trait. On the other hand, better agricultural land management, use of fertilizers, safe and efficient pesticides and herbicides, farm mechanization, and transgenic crop usage (Glick 2014) are the solutions to increase the agricultural productivity, but they give only short-term benefits. For an effective and long-term solution to provide food for the world, sustainable and eco-friendly biological solutions have to be implemented. Promising measures include use of microbial inoculants which can ameliorate stress, promote growth, control diseases, and contribute to the development of sustainable agriculture (Berg et al. 2013). Plant growth-promoting rhizobacteria (PGPR) colonize the rhizosphere/endorhizosphere of plants and promote growth of the plants through various direct and indirect mechanisms (Ramadoss et al. 2013).

The use of PGPR as an alternative to alleviate abiotic plant stress is gaining importance (Dodd and Perez-Alfocea 2012) (Table 4.4). The ability of PGPR to induce stress tolerance is often attributed by various processes that involve physiological and biochemical changes. It includes modifications in phytohormonal content (Kaushal and Wani 2016), antioxidant defense (Jyothsna and Murthy 2016), osmolyte production (Diby and Harshad 2014), ACC deaminase activity (Yang et al. 2009), and biofilm formation (Vanderlinde et al. 2010; Yang et al. 2009). Rhizobacteria often induce modifications in phytohormone signaling, which mediates effects on meristem activity (Hayat et al. 2010). Saravanakumar et al. (2011) and Sandhya et al. (2010) have suggested the possible role of PGPR to alleviate the oxidative damage elicited by abiotic stress through the manipulation of antioxidant enzymes in different crops. The beneficial effects of PGPR to reduce adverse effects of salinity have been demonstrated in tomatoes (Kidoglu et al. 2008), bell peppers, cucumbers (Kidoglu et al. 2008), radish (Yildirim et al. 2008), barley (Cakmakci et al. 2007), tobacco, mustard (Asghar et al. 2002), and eggplant (Bochow et al. 2001). Several studies indicate that plants require microbial association for stress tolerance (Egamberdieva and Jabborova 2013). Rabie et al. (2005) reported increased N and P nutrition, increased nodulation, and nitrogenase activity in AM fungi and N-fixer *Azospirillum brasilense*-treated cowpea plant at different NaCl salinity levels. Application of *Pseudomonas chlororaphis* (TSAU13) to tomato and cucumber promoted growth and fruit yield in saline soil and also reduced the incidence of disease caused by *Fusarium solani* (Egamberdieva 2012). Basha and Vivekanandan (2000) isolated a salt-tolerant rhizobial strain from tannery sludge which successfully nodulated cowpea in saline soils (250 mM NaCl).

High salinity suppresses the phosphorus (P) uptake by plant roots and reduces the available P by sorption processes (Vivekanandan et al. 2015). PGPR strains having efficient P solubilizing ability even under high saline (60 g/l NaCl) conditions have been reported (Upadhyay et al. 2011). Gibberellins secreting *Pseudomonas putida* H-2-3 improved plant growth in soybean under drought conditions (Sang-Mo et al. 2014). The other mechanism by which PGPR facilitates the growth of plants is the secretion of 1-aminocyclopropane-1-carboxylate (ACC) deaminase. This enzyme decreases plant ethylene level and diminishes negative effects caused by stress condition (Glick 2014). The ACC deaminase activity of *Achromobacter piechaudii* was shown to confer drought tolerance in

Table 4.4 Role of PGPR in alleviating salinity and drought stress

PGPR strain	Plants	Stress factor	PGP activity	Reference
Enterobacter sp.	Okra	Salinity	ACC deaminase	Habib et al. (2016)
Phyllobacterium	Strawberries	Salinity and drought	Phosphate solubilization, siderophore production	Flores-Felix et al. (2015)
Burkholderia cepacia and *Promicromonospora* sp.	Cucumber	Salinity and drought	Increased gibberellic acid, salicylic acid	Sang-Mo et al. (2014)
Streptomyces sp. strain PGPA39	Tomato	Salinity	Increased ACC deaminase activity, IAA production, and phosphate solubilization	Palaniyandi et al. (2014)
Chryseobacterium	Tomato	Salinity and drought	Siderophore production	Radzki et al. (2013)
B. licheniformis K11	*Capsicum annuum*	Drought	Ethylene concentration reduction	Lim and Kim (2013)
Brevibacterium iodinum, *Bacillus licheniformis*, *Zhihengliuela alba*	Red pepper	Salinity	ACC deaminase	Siddikee et al. (2011)
Bacillus	Alfalfa	Salinity and drought	Antibiotic production	Sokolova et al. (2011)
P. putida UW4 and *Gigaspora rosea* BEG9	Cucumber	Salinity	ACC deaminase	Gamalero et al. (2010)
Pseudomonas sp.	Eggplant	Salinity	Antioxidant enzymes	Fu et al. (2010)
P. mendocina	*Lactuca sativa*	Salinity	Water content was greater in leaves of plants, higher concentrations of foliar K, and lower concentrations of foliar Na	Kohler et al. (2009)
B. subtilis	Tomato	Drought	Cytokinin signaling	Arkhipova et al. 2007)

tomato and pepper, resulting in significant increases in fresh and dry weights with a decrease in ethylene level (Mayak et al. 2004). Another ACC deaminase-positive PGPR strain, *A. piechaudii* ARV8, conferred IST (induced systemic resistance) to drought stress in pepper and tomato plants (Mayak et al. 2004). Furthermore, tomato plants inoculated with ACC deaminase producing

Pseudomonas fluorescens YsS6 and *P. migulae* 8R6 had higher fresh and dry biomass and higher chlorophyll content than the ACC deaminase-negative bacteria-treated tomato plants, grown with 165 mM and 185 mM of salt (Ali et al. 2014). In a similar investigation, cucumber plants inoculated with *P. putida* UW4 and *Gigaspora rosea* BEG9 and grown at 72 mM salt concentration showed significantly higher root and shoot fresh biomass than uninoculated plants (Gamalero et al. 2010). Co-inoculation of lettuce with PGPR *Pseudomonas mendocina* and AM fungi (*Glomus intraradices* or *G. mosseae*) augmented the antioxidant catalase activity under severe drought conditions suggesting that they can be used as inoculants to alleviate the oxidative damage elicited by drought (Kohler et al. 2008). Also, *A. piechaudii*, which produced ACC, increased the growth of tomato seedlings by 66% in the presence of high salt contents (Choudhary et al. 2011). Tank and Saraf (2010) reported phosphate solubilization, phytohormones, and siderophore production in tomato plant under 2% NaCl stress by PGPR.

Proline is often synthesized by plants in response to various abiotic and biotic stresses, mediating osmotic adjustment, free radical scavenging, and subcellular structure stabilization (Hare and Cress 1997). Increased proline synthesis has been shown in abiotically stressed plants in the presence of beneficial bacteria. Modifications of plant morphogenetic parameters and increased efficiency of photosynthesis was induced by AM fungi in salt conditions (Gamalero et al. 2009). Kohler et al. (2009) investigated the influence of inoculation with a PGPR, *P. mendocina*, alone or in combination with an AM fungus, *G. intraradices* or *G. mosseae*, on growth and nutrient uptake and other physiological activities of *Lactuca sativa* affected by salt stress.

Chookietwattana and Maneewan (2012) selected 84 halotolerant bacterial strains and assessed their phosphate-solubilizing activity. Of these, *Bacillus megaterium* A12 was selected as the efficient halotolerant PSB because it demonstrated the highest phosphate solubilization activity under saline conditions. The *B. megaterium* A12 significantly increased the germination percentage and germination index of tomato seeds grown with NaCl concentrations between 30 and 90 mM and increased the seedling dry weight at NaCl up to 120 mM. Their results suggest that the halotolerant PSB may be used to alleviate the effects of salts and provide great potential for use as biofertilizers in the arid and salt-affected areas. Wang et al. (2012), when tested the effect of PGPR strain BSS on cucumber plant against drought tolerance, reported induction of systemic resistance in cucumber plant. Other workers have also reported that the stomatal conductance of plant leaf was higher in PGPR *Pseudomonas aeruginosa*-inoculated mung bean plants than non-PGPR inoculated ones under drought conditions (Ahmad et al. 2013, Sarma and Saikia 2014, and Naveed et al. 2014). Nautiyal et al. (2008) demonstrated that the *Bacillus lentimorbus* strain increased the antioxidant capacity of the edible parts of spinach, carrots, and lettuce, as well as increase in growth. Yildirim et al. (2008) studied the ameliorative effect of *Staphylococcus kloosii* strain EY37 and *Kocuria erythromyxa* strain EY43 on radish growing in saline soil. They observed that bacterial inoculants significantly increased shoot/root dry weight, leaf number per plant, relative water content of the leaf, and chlorophyll content of radish fruit. Corn, beans, and clover inoculated with AM fungi had increased proline content which resulted in salinity resistance (Grover et al. 2011).

Conclusion

Salinity and drought stress are the serious environmental issues which drastically reduce the productivity of vegetables. The use of plant growth-promoting microorganism in vegetable crop production has received little attention. Enhancement in the use of PGPR is one of the newly emerging options to meet the agricultural challenges imposed in the stresses in soil environment. Few reports which are available today have shown that PGPR could improve plant productivity even in stressed environment by counteracting the negative effects of saline and water stresses on plant growth. PGPR promote the growth of plants through variety of mechanisms like triggering osmotic response, providing growth hormones and nutrients, acting as biocontrol agents, and modifying root to shoot signaling in plants. Developing salt-tolerant crops is still in the pipeline, and therefore, the only viable alternative seems to be the use of PGPR for enhancing vegetable production under stressed environment. The complex and dynamic interactions between microorganisms and plant roots under conditions of abiotic stress affect not only the plants but also the physical, chemical, and structural properties of soil. Selection of microorganisms from stressed ecosystems and their possible application under stressed conditions to mitigate the impact of abiotic stresses are likely to improve the production of vegetables in soils stressed with different abiotic factors.

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