



SALT TOLERANT BACTERIA FOR CROP IMPROVEMENT IN SALINE AGRICULTURE FIELDS: DEVELOPMENT, CHALLENGES AND OPPORTUNITIES

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Abstract

Saline stress has been the one of the biggest hurdles in achieving the demand and supply ratio of global population. To combat the growing problem of soil salinity, advanced soil management and irrigation technology are used. However, they are cost and energy intensive. Plant growth promoting rhizobacteria (PGPR) attained from saline soils can overcome the detrimental effects of salt stress on plants. PGPR positively impact physiological functions of plants such as growth, yield and overcome disease resistance. The complex and dynamic interface between microorganisms and plant roots is achieved by various mechanisms like secretion of plant growth hormones, pigments and decrease of oxidative stress. Thus, PGPR can be used as an alternative to improve yield of crops from saline lands. This review is an attempt to provide the current status on the PGPR from salt inflicted soils and their application for growing crops in saline soils.

Key words: plant growth promoting rhizobacteria, salt tolerant bacteria, halophiles, agriculture, crop improvement, saline fields

Introduction

The world population was estimated approximately 7.8 billion people. Globally, this is projected to rise up to 9.7 billion by 2050. The drastic increase in world population increased the demand of food products (Mesa-Marín *et al.*, 2019). The crop production per unit of land cultivated is sluggish to meet the predicted demand for food. Besides change in climate, loss of soil structure, nutrient degradation, drought and soil salinity (Khan *et al.*, 2019b; Mukhtar *et al.*, 2019) are the major factors behind the decreased crop yields (Ma *et al.*, 2019a). Global warming, depletion of water resources (drought stress) (Zafar-ul-Hye *et al.*, 2019b), poor quality of irrigation water, improper soil water-crop management etc. lead to severe issue of saline soil (Mahpara *et al.*, 2019) (salt concentration more than 200 mM). Food and Agricultural Organization (FAO), manifested a worldwide loss of 50% land of total land mass by the year 2050. Excess salt leads to the decreased plant growth and deregulated metabolism (El-Ramady *et al.*, 2019b). Free radical generation (Mesa-Marín *et al.*, 2018) such as

superoxide radical, hydrogen peroxide (H₂O₂) and singlet oxygen, decrease in plant defensive enzymes, imbalance in sodium hemostasis, decreased iron uptake, phenols and other trace elements are the manifestations seen in the saline stress (Korres *et al.*, 2019; Tully *et al.*, 2019). Soil salinization process has been described in fig. 1.

In recent time, various approaches have been employed to solve the salinity and acidity in soil (Acuña Rodríguez *et al.*, 2019; Costa *et al.*, 2018; El-Ramady *et al.*, 2019a; Gangwar *et al.*, 2020; Jo and Pak, 2019). Development of salt-tolerant crops through breeding, physical removal of salts from the surface of soil and chemical treatment of soil are some of the techniques established by scientists (Cuevas *et al.*, 2019; Safeena and Zakeel, 2019; Safikhani *et al.*, 2018). These methods have complexity in tools or techniques as presented in fig. 1 (Gupta *et al.*, 2018). Alternative methods for retrieval of salt affected soils include phytoremediation and bioremediation (Agrawal *et al.*, 2018; Kumar and Verma, 2019; Mishra *et al.*, 2019). These large scale organic farming methods use the halotolerant plants and salt tolerant bacteria, respectively (Kumari, 2018; Singh

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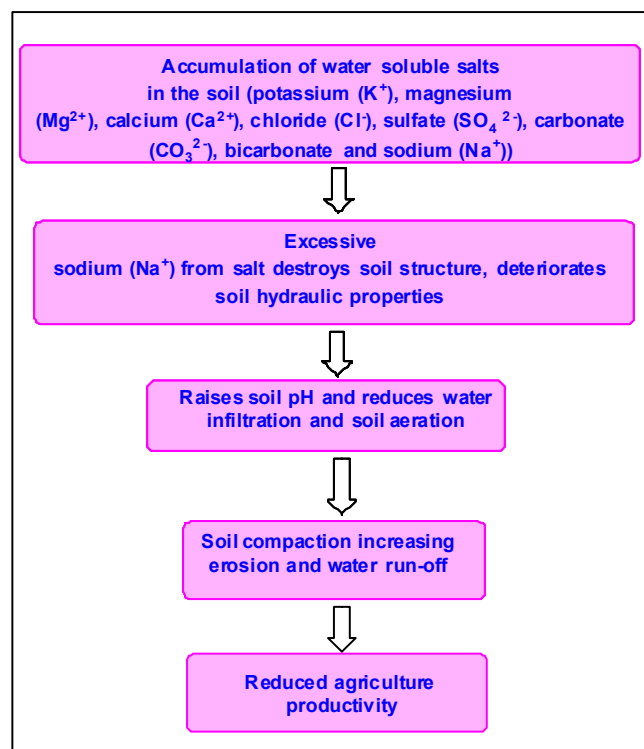


Fig. 1: Process of soil salinization that leads to loss of agriculture productivity.

et al., 2019c). Plant growth promoting rhizobacteria (PGPR) are the symbiotic heterogenous bacteria which are known as one of the beneficial root-associated bacteria (Kenneth et al., 2018; Meena, 2018; Yasmeen et al., 2019). The bacteria act as biofertilizers and recycle the plant nutrients which leads to phytostimulation and

phytoremediation (Ullah and Bano, 2019; Zhang et al., 2018). These can be intracellular or extracellular. *Klebsiella*, *Pseudomonas*, *Rhizobium*, *Azospirillum*, *Enterobacter*, *Serratia*, *Alcaligenes*, *Arthrobacter*, *Azotobacter*, *Burkholderia* and *Bacillus* are the bacterial species encompassing plant growth promoting rhizobacteria (Chennappa et al., 2018; Ipek et al., 2019; Sarkar et al., 2018b; Sayyed et al., 2019b; Zhang et al., 2018). The bacteria can enter through root hair (endophytic bacteria) or can reside on the root surface (rhizosphere bacteria) and act as bio-organic manure (Choudhary et al., 2019; Kumari et al., 2019; Vaishnav et al., 2018; Vaishnav et al., 2019). They produce and increase the concentration of siderophores exopolysaccharides, (Paul et al., 2019) alter pH, modify toxic metals, (Mousavi et al., 2018) solubilize phosphorus (Kadmiri et al., 2018) and calcium, evacuate stress-alleviating metabolites (1-aminocyclopropane-1-carboxylic acid deaminase), (Bharti and Barnawal, 2019) secrete indole-3-acetic acid (IAA) (Yousef, 2018), cytokinin and gibberellins and provide resistance of antibiotics as presented in fig. 2 (Barnawal et al., 2019; Li and Liu, 2019; Saghafi et al., 2019a; Singh, 2018).

Inoculation with PGPR has been known to modulate abiotic stress regulation via direct and indirect mechanisms that induce systemic tolerance (Govindasamy et al., 2018; Rani et al., 2018; Sagar et al., 2019; Zaheer et al., 2019). In recent past, a large number of PGPR have been identified attributing their role in the rhizosphere as an ecosystem and their potential as biofertilizer (Chandra et al., 2019; Liang et al., 2018; Thennarasu et al., 2019). Root-associated bacteria are more tolerant to salt stress than soil bacteria, since salinity stress is higher in the rhizosphere due to depletion of water by the plant root, resulting in a local increase in both ionic strength and osmolality (Dubey et al., 2020; Kumar et al., 2019b). Salinity negatively affects microbiological activity of soil by high osmotic strength and toxic effects of salts on microbial growth can occur, with the exception of tolerant halophytic bacteria (Jyothi et al., 2018). Therefore, salt tolerant plant growth-promoting bacteria, like *Azotobacter chroococum*, *Pseudomonas aeruginosa* PF23 and *Serratia marcescens* can survive in such harsh environments (Cabot et al., 2018; Kumar et al., 2018b; Mishra et al., 2018).

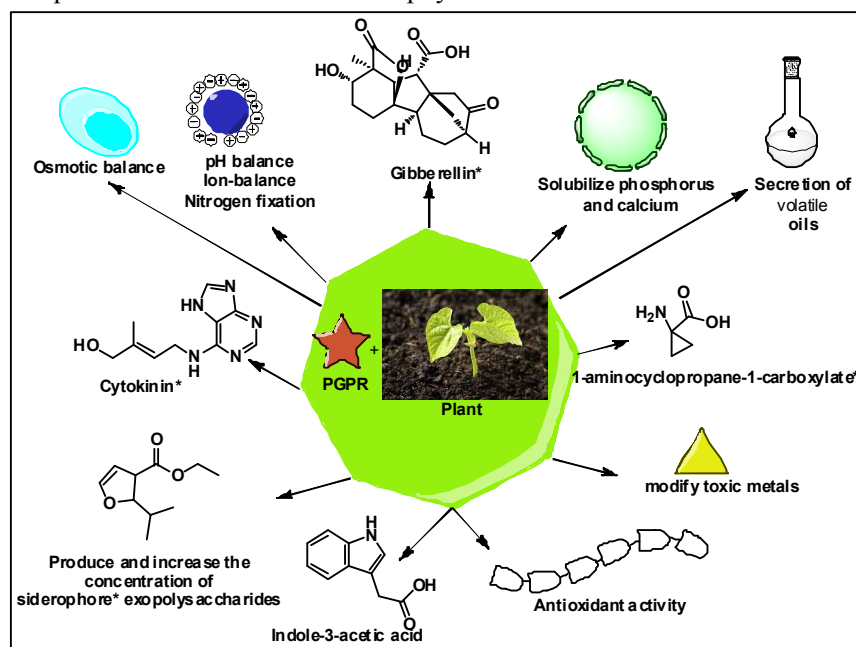


Fig. 2: A representative class of metabolites produced by plant growth-promoting rhizobacteria (PGPR). * There are various other members of each class. Only representative molecules have been shown in the diagram.

Soil salinity

Soil salinity affects extensive areas of land in both developed as well as in developing countries (Yoo *et al.*, 2018). The agricultural intensification, together with unfavorable natural conditions, has accelerated soil salinity in several parts of the world (Arora and Dagar, 2019; Srivastava *et al.*, 2019). With insufficiency of good quality irrigation water and rising pressure of producing more from every hectare of available arable land, the poor-quality groundwater has been increasingly used for irrigation. Worldwide farming utilizes approximately 70% of ground water but its depletion lead to the poor-quality water being utilized in farming (Dalin *et al.*, 2019; Majeed and Muhammad, 2019). Many more areas with good quality aquifers are endangered with contamination as a consequence of excessive withdrawals of groundwater. Indiscriminate use of poor-quality waters in the absence of proper soil water-crop management practices poses grave risks to soil health and environment. Development of salinity, sodicity, acidity, water-logging and toxicity problems in soils not only deteriorates the quality and quantity of produce and limits the choice of cultivable crops, many a times the effects become so severe that lands eventually go out of cultivation (Abod *et al.*, 2019; Osman, 2018). Salt affected lands occur over varied geological formations, in all kinds of soils and under different conditions of climate and human interventions and accordingly, their extent, characteristics and response to management are highly variable (Gregory *et al.*, 2018; Kumar *et al.*, 2019a). For practical usage, salt-affected lands have been identified as saline, alkali, sodic, (Hafeez) saline-alkali (Kumar *et al.*, 2018a) or saline sodic (Pankaj *et al.*, 2019; Shao *et al.*, 2019). Saline soil has an excess of soluble salt in the soil solution, the liquid located between aggregates of soil (Etesami, 2018; Lamizadeh *et al.*, 2019). Sodic soil has too much sodium associated with the negatively charged clay particles (Shahnaz and Manjurul, 2018). Salinity occurs through natural or human-induced processes that result in the accumulation of dissolved salts in the soil water to an extent that inhibits plant growth (Powrie, 2018; Saghafi *et al.*, 2019b). High salinity in soil induces ionic and osmotic stress, (Mukhtar *et al.*, 2018; Munns *et al.*, 2020) resulting in growth retardation through malfunctioning photosynthesis and ion homeostasis (Daliakopoulos *et al.*, 2016; Liu *et al.*, 2019; Majeed *et al.*, 2019). Currently, 1,125 million hectares area is salt affected, out of which salinity in 76 million hectares is human-induced (Hossain, 2019; Sayyed *et al.*, 2019a).

On the other hand, when plant cells are exposed to salinity mediated by high NaCl concentrations, the steady

states kinetics of ion transport for Na⁺ and Cl⁻ and other ions, such as K⁺ and Ca²⁺ are disturbed (Bashandy *et al.*, 2019; Yang and Guo, 2018). It is generally accepted that plant cells must maintain a high ratio of K⁺ and Na⁺ ions in their cytoplasm if they are to grow successfully in saline environments (Wu, 2018; Yun *et al.*, 2018). Salinity affects physiology of plant through changes of the ionic status in the cells (Bosnic *et al.*, 2018; Parasuraman *et al.*, 2019). Thus, it is vital for the plant to re-establish cellular ion homeostasis for metabolic functioning and growth and to adapt to the saline environment (Ren *et al.*, 2018; Wu, 2018). Presently, it is widely assumed that the death of plant cells exposed to saline conditions is caused by a high ratio of Na⁺ and K⁺ ions in the cytoplasm, which is due to drastic increases in the influx of Na⁺ ions into the cells and in the efflux of K⁺ ions from the cells (Rubio *et al.*, 2020). Under saline conditions, the large electrochemical Na⁺ gradient results in passive Na⁺ uptake into root cells (Selvakumar *et al.*, 2018; Singh *et al.*, 2019b). The essential role of Ca²⁺ ions have been extensively documented with respect to various cellular functions that are associated with the growth and development of plants (Parvin *et al.*, 2019; VanWallendael *et al.*, 2019). In particular, regulation of membrane functions is thought to be one of the most important roles of Ca²⁺ ions in plant cells (DA WEI *et al.*, 2019; Guo *et al.*, 2019). Ca²⁺ is known to have better effects on plants under high-salinity conditions and also was known to decrease low-affinity Na⁺ uptake (Sun and Zhou, 2018). Various plant nutrients have their roles under saline conditions (El-Ramady *et al.*, 2018).

Paradigm of mitigation of salt stress: Recent literature on the role of PGPRs

Global increase in soil salinization constitutes the most devastating environmental threat for crop yield and food quality (Rahman *et al.*, 2019; Tyerman *et al.*, 2019). Soil salinity has been recognized worldwide as one of the major limitation for crop production in arid and semiarid regions (Dong *et al.*, 2019; Ivushkin *et al.*, 2019). Groundwater continuously moves towards the cultivation layer and the concentration of soluble salts increases due to the recycling of poor-quality water for irrigation (Machado and Serralheiro, 2017). Sodic and saline soil is reducing the cultivable area for agriculture by 1-2% every year, thereby reducing food production (Etesami and Beattie, 2018; Hayes *et al.*, 2019). The primary concern regarding saline soil is its impact on plant growth (Hayes *et al.*, 2019). Excessive salt concentration (more than 200 mM) inhibits plant growth (Mukhtar *et al.*, 2018; Shahid *et al.*, 2018) and affects many aspects of plant metabolism, resulting in reduced growth and yield

(Chaowanaprasert *et al.*). Physical removal of salts from the surface of soil or chemical treatment of soil is not only expensive, but also impractical to vast areas for soil reclamation purposes (Damodaran *et al.*, 2019). Many scientists have attempted to develop salt-tolerant crops through breeding, but these efforts have met with limited success due to the genetic and physiological complexity of the salt tolerance traits (Seido *et al.*, 2019; Tolba *et al.*, 2019). Thus, phytoremediation (i.e. using the halotolerant plants) and bioremediation (using the salt tolerant bacteria) are alternatives for reclamation of salt affected soils on large scale (Lata and Gond, 2019; Schillaci *et al.*, 2019; Yilmaz and Kulaz, 2019). Dry weight, wet weight, root length and shoot length was increased by PGPR (Sulthana *et al.*, 2018). The PGPR in plant growth promotion have been covered by various authors in literature; including Numan *et al.*, (2018); Siyar *et al.*, (2018) and Abbas *et al.*, (2019) (Abbas *et al.*, 2019); Prasad *et al.*, (2019) (Prasad *et al.*, 2019); Bilinski *et al.*, (2019) (Bilinski *et al.*, 2019), Kashyap *et al.*, (2019) (Kashyap *et al.*, 2019), Bhatt *et al.*, (2019) (Bhat *et al.*, 2019), Altaf *et al.*, (2019) (Altaf *et al.*), Siyar *et al.*, (2019) (Siyar *et al.*, 2019) and IAsif *et al.*, (2019) (Asif *et al.*, 2019). In this review, we intended to include the mechanism of PGPR's, the types of PGPR's, recent research paradigms in PGPR's and salinity, combination treatment of PGPR's with other agents and products etc. The most recent literature findings demonstrating the role of PGPR's based on mechanism in cultivation of different plants have been covered.

• Nitrogen fixation:

A study by Reginawanti *et al.*, (2019) explored the *Azotobacter* resistance (K4, S2 and S1) for sodium chloride in tomato seedling. Results revealed that this resistance was higher in the S2 and K4. Authors established that the plausible effect was might be due to the osmotic adjustment. Further addition of 2% glycerol amplified this effect. Leaf number and root dry weight was increased by this inoculation (Hindersah *et al.*, 2019).

Another study by Noori *et al.*, (2019) isolated rhizobial and non-rhizobial drought and salinity tolerant bacteria from the surface sterilized root nodules of alfalfa, grown in saline soils and evaluated the effects of effective isolates on plant growth under salt stress. They co-inoculated the alfalfa plant with *Klebsiella* sp. A36, *K. cowanii* A37 and rhizobial strain *S. meliloti* ARh29. The results demonstrated that *Klebsiella* sp. A36, *Kcowanii* A37 could deliver plant nitrogen and upsurge plant growth indices without rhizobial bacteria and nitrogen (Noori *et al.*, 2018).

• Phosphorus-solubilization and siderophore production:

Bacillus (SB1) and *Halobacillus* (SB2) isolated from groundnut rhizosphere had shown the ability to overcome the salt and metal stress (Banik *et al.*, 2018). Mahmood *et al.*, (2019) isolated, screened and characterized rhizosphere bacteria from the common ice-plant *Mesembryanthemum crystallinum* L. A total of 80 out of 152 strains displayed tolerance to soil salinity. *Streptomyces* sp. PR-3 and *Bacillus* sp. PR-6 were effective against soil salinity (< 1250 mM NaCl). The soil salinity mitigation by *Streptomyces* sp. strain PR-3 was done through phosphorus solubilization whereas siderophore production was shown by *Bacillus* sp. strain PR-6 PR-3 and PR-6 showed IAA production. In addition, authors established that these bacteria have the ability to promote growth in the common ice-plant (Mahmood *et al.*, 2019). Shobhit and research group established a comparative study of *Bacillus* sp. and *Pseudomonas* sp. on wheat under saline conditions. *Bacillus* sp. enhanced plant height (32.32%), root length (37.84%), fresh weight (28.2%) and dry weight (15.51%). This increase was more potent than the *Pseudomonas* sp. (Vimal *et al.*, 2018)..

The potential of *Bacillus* sp. has been escalated in combination with various agents. *Bacillus cerus* in combination with tryptophan was established to be more potent in the growth of wheat (HASSAN12 *et al.*, 2018). The combination of PGPR's, phosphate sources and vermicompost has been demonstrated to be useful in growth and nutrient uptake by plants under saline stress (Khosravi *et al.*, 2018). Behzad *et al.*, (2019) demonstrated improved growth and salinity tolerance of the halophyte *Salicornia* sp. by co-inoculation with endophytic and rhizosphere bacteria. They evaluated drought tolerance of salt-tolerant isolates, performed 1-aminocyclopropane-1-carboxylate (ACC)-deaminase, IAA production and phosphate solubilization assay etc. E14, E221, R11, R218 and R21 were the endophytic and rhizosphere isolates produced ACC deaminase. The E14 and R11 strains displayed significant inorganic solubilization of phosphate and displayed IAA production (2.9 and 3.9 $\mu\text{g mL}^{-1}$ respectively) under saline conditions. Authors established that when halophyte *Salicornia* sp. was co-inoculated with rhizosphere and endophytic bacterial strains in 200 mM NaCl, the morphological parameters of the halophyte *Salicornia* sp. exhibited substantial results except for root length. Further, the chlorophyll content was escalated as compared to control, sodium content was decreased, potassium and potassium to sodium ratio in plant aerial parts were increased.

Authors concluded that endophytic and rhizosphere isolates associated with the halophyte *Salicornia* sp. are drought and salinity resistant and *Staphylococcus* bacteria exhibited the high salt tolerance (Komaresofla *et al.*, 2019).

Sangeeta *et al.*, (2019) reported the ACC deaminase producing bacteria for the reduction of salt stress in *Allium sativum*. These isolates were screened for their ability to utilize ACC as nitrogen source on DF minimal salts medium. Six strains were found to be positive as ACC deaminase producing bacteria (strains ACC02, ACC04, ACC06, ACC07, ACC011 and ACC012). Two isolates ACC02 (*Aneurinibacillus aneurinilyticus*) strain AIOA1 and ACC06 (*Paenibacillus* sp. strain SG_AIOA2) indicated higher ACC deaminase activity as compared to other selected ACC deaminase producers (1677 and 1589 nmol α -ketobutyrate mg protein⁻¹ h⁻¹, respectively). The bacteria converted nitrogen source ACC into α -ketobutyrate. Further maximum solubilization of phosphate was shown by ACC02 (86.25mg/L). The generation of organic acids lowered the pH. These potent ACC deaminase producers were assessed for root growth promotion by pot experiments. The research done with sterilized French beans (*Phaseolus vulgaris* L.) variety (*AkraKomal*) seeds found that consortia (ACC02+ACC06) treated seeds displayed significant increase in length and fresh weight of roots and shoots as well in chlorophyll content as compared to uninoculated (control) seeds as well as individually bioprimered seeds (Pandey and Gupta, 2019).

Muhammad *et al.*, (2019) documented effects of W10 (*Serratia ficaria*), W14 (*Pseudomonas fluorescens*) and 6K on production of wheat under saline situations. The treatment design consisted of control, W10, W14, 6K, W14 \times W10, W14 \times 6K, W10 \times 6K and

W14 \times W10 \times 6K. Three soil salinity levels were considered: 3 dS m⁻¹, 6 dS m⁻¹ and 9 dS m⁻¹. The best results on number of spikelets (14.93), root length (11 cm), shoot length, (75.5 cm), dry shoot weight (1.13 g) and dry root weight (0.52 g) at EC 3 dS m⁻¹ were found in W14 \times W10 \times 6K. Further the same design produced maximum number of grains, maximum biological yield (200.19 per pot at EC dS m⁻¹) and maximum number of tillers (4.73/plant). The inoculation lead to the increase in nitrogen, phosphorus and potassium. ACC-deaminase was concluded to be the reason behind increased production of the wheat (Zafar-ul-Hye *et al.*, 2019a).

- Multiple cascades: Antioxidant activities, osmotic balance, IAA and ACC production:

Nizar *et al.*, (2019) characterized native bacteria from the saline rhizosphere of *Sulla carnosa* and established rhizobacteria isolates which escalate the salt tolerance of *Sulla* sp. *Acinetobacter* sp. (Br3), *Pseudomonas putida* (Br18) and *Curtobacterium* sp. (Br20) were explored as PGP's. Salt tolerance capacity and plant growth promoting ability were detected. Isolation of 26 rhizobacterial isolates was followed by microscopic examination and detection of salt tolerance capacity and plant growth promoting abilities. The study established that high salt concentrations lead to the increased proline, total soluble sugar content and cell membrane injury. Plant growth promoting microbial isolates demonstrated escalation in Ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX) and antioxidative enzymes under saline environment (Fig. 3) (Hmaeid *et al.*, 2019). The results suggested increased biomass and potassium levels as well as reduced malondialdehyde (MDA) and leakage of electrolyte. Compatible solutes were suggested to reduce the high osmolarity stress. Also, *Curtobacterium albidum* strain SRV4 and *Pseudomonas* sp. UW4 had shown plant growth promoting potential in rice and tomato plants in previous studies (Orozco-Mosqueda *et al.*, 2019; Vimal *et al.*, 2019). In another study, Singh *et al.* explored the native sunflower ACCd producing PGPR to induce the salt stress tolerance in *Helianthus annuus* L. and evaluated the physiological and biochemical variations occurring in saline conditions. The APX assay, superoxide dismutase (SOD) assay and proline estimation were performed, with MDA determination. *Pseudomonas otitidis* Rhizo SF 7 (IC₅₀=13.44) and *Acinetobacter*

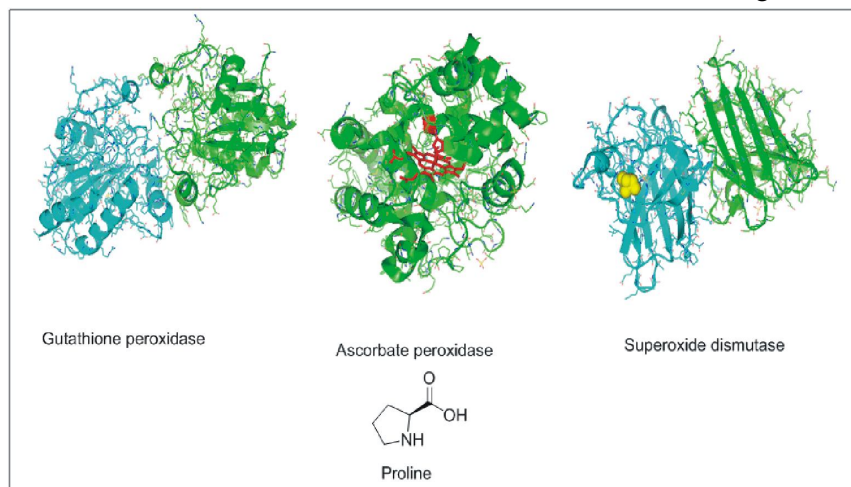


Fig. 3: Structures of Glutathione peroxidase, ascorbate peroxidase, superoxide dismutase and proline produced by PGPR.

Pseudomonas otitidis Rhizo SF 7 (IC₅₀=13.44) and *Acinetobacter*

calcoeticus RhizoSF 9 ($IC_{50}=11.26$) showed the maximum salt tolerance. Further PGPR's increased plant height, shoot fresh weight, dry weight and total chlorophyll under the stress conditions. Authors established that proline content had been augmented in ACCd generating PGPR treated seeds. The increase in APX activity and maximum SOD enzyme activity in Rhizo SF 7 treated sunflower with stress was 0.5 fold and $23.84 \text{ U min}^{-1} \text{ mg}^{-1}$ respectively. When compared to control, MDA content was decreased in Rhizo SF 7 and Rhizo SF 9 treated seedlings under salt stress (Singh et al., 2019a).

Izzeddine et al., (2019) evaluated the capacity of *Pseudomonas plecoglossicida* strain Pp20 to mitigate the damages on maize roots caused by salt and aluminum. Pp20 has shown its ability to grow at varied NaCl concentrations from 50-600 Mm and fresh mass and dry mass were increased to 48% and 102%, respectively. The results revealed a positive impact on stem weight, seminal roots, lateral roots and root length. Additionally, PGPR treatment also increased the concentration of chlorophyll (32%) and carbohydrate (93%). The study attributed that this *Pseudomonas plecoglossicida* strain Pp20 generated ACC deaminase and damaged the plant hormone ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC). Furthermore, the production of IAA had been established (Zerrouk et al., 2019). Bioaugmentation of microbial strains may help as a favored strategy for refining phytoremediation of metal polluted saline soils.

Ying et al., (2019) studied and reported the impact of *Pseudomonas libanensis* TR1 on *Helianthus annuus*. *P. libanensis* exhibiting high resistance against saline stress (8%) (Ma et al., 2019b). Bacillus SB1 and HalobacillusSB2 strains were explored in various combinations with metals (Zinc, aluminium and lead) in the growth of *Arachis hypogaea* L. under saline stress by Avishek et al., (Banik et al., 2018). Various pigments were isolated from the both strains. Methyl 5-oxopyrrolidine-2-carboxylate, Trideca-1, 12-dien-3-one, 2-Acetamido-3-cyanopropanoic acid, Ethyl 2-isopropyl-2,3-dihydrofuran-3-carboxylate, Methyl undec-10-ynoate, 1-(3,4-Dihydropyridin-1(2H)-yl)ethan-1-one, Methyl (E)-tetradec-10-enoate were isolated from SB2. SB1 was responsible for the generation of pentadecanoic acid, bis (2-ethylhexyl) phthalate and squalene (Fig. 4).

Jacqueline et al., (2019) explored ACCd-producing rhizobacteria from *Pseudomonas quadrangularis* under saline stress and studied the effects of PGPR on wheat seedlings (*Triticum aestivum* L.). The pot experiment was carried under the green house conditions and it was established that the isolates from the *P. quadrangularis* had ACCd activity. Conventionally, the ACCd producing isolates ($0.83\text{-}3.32 \mu\text{mol } \alpha\text{-ketobutyrate mg}^{-1}\text{h}^{-1}$) were belonging to the *Serratia* and *Klebsiella*. These isolates produced auxins (20.3 to $41.0 \mu\text{g mL}^{-1}$) and siderophores. Additionally, inoculation of *Klebsiella* isolates (8LJA and 27IJA) with wheat seedlings, the biomass content and SOD activity in roots were escalated (45-62% and 18-

35% respectively) with and without saline stress conditions (Acuña et al., 2019). However, *Klebsiella* IG3 strain had already been established as a growth promoter in the *Avena sativa* seedlings by Swapnil and co-workers (Sapre et al., 2018).

Sang et al., (2019) reported the role of *Leclercia adecarboxylata* MO1 in *Solanum lycopersicum* L. growth and salt stress tolerance by endogenous secondary metabolites regulation. Under saline stress conditions, *L. adecarboxylata* MO1 treatment increased the shoot weight and length (70.71% and 39.83% respectively), root length and weight (21.38% and 82.72% respectively) and diameter of stem (21.04%). Further, MO1 treatment leads to the increased chlorophyll stress-responsive endogenous ABA. Authors reported the escalation in glucose

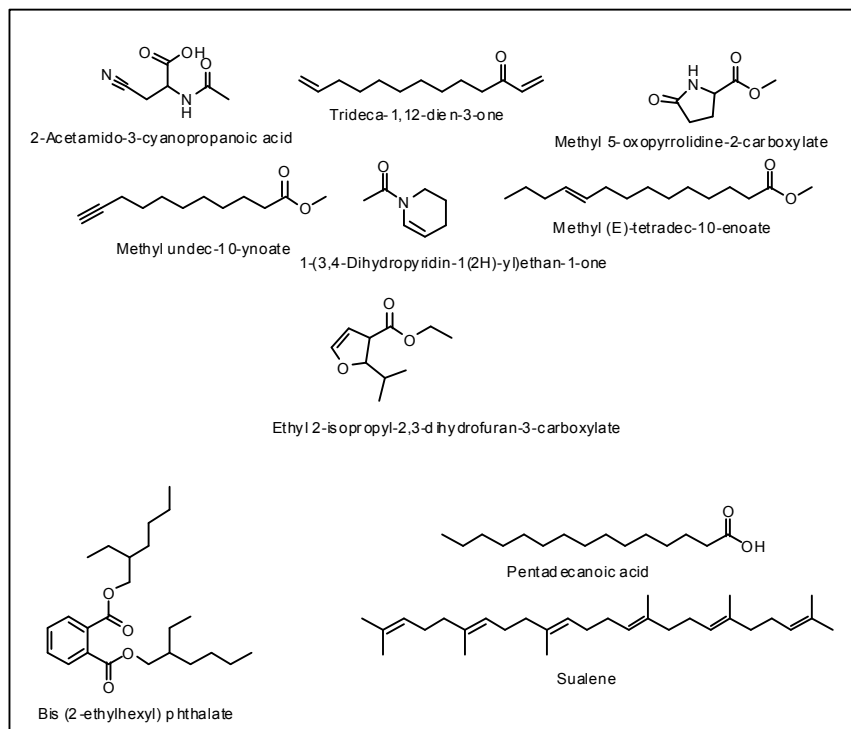


Fig. 4: Chemical structures of various pigments isolated from the SB1 and SB2.

(17.57%), fructose (19.9%), sucrose (34.2%), citric acid (47.48%) and malic acid (52.19%) in MO1 treated *Solanum lycopersicum* L. under salt stress conditions (Kang *et al.*, 2019). In another study, Muhammad *et al.*, (2019) described the efficiency of salt-tolerant plant growth-promoting endophytes (PGPEs) *Kocuria rhizophila*: KF875448 (14ASP) and *Cronobacter sakazakii*: EF059843 (OF115), ACC deaminase production, role of osmolytes and antioxidant enzymatic activity on the development of *Triticum aestivum* L. plants (Pasban 90 and Khirman) under several saline conditions. Siderophores were produced after inoculation of both strains. Under salt stress, chlorophyll content, root length, fresh biomass, leaf water potential, shoot length, dry biomass of Khirman and Pasban 90 were escalated by *K. rhizophila* and *C. sakazakii*. Further the inoculation showed increase in the SOD and CAT antioxidant activities, proline content, K^+ , Mg^{2+} and Ca^{2+} contents in the shoots and decrease in shoot Na^+ concentration (Afridi *et al.*, 2019).

Mitra *et al.*, (2019) showed that the growth and better yield of barley by inoculation with *Pseudomonas fluorescens* (B10, B2-10, B2-11 and B4-6) under saline conditions. Under saline stress, there was an increase in the plant height, grain yield, spike length, MGW, number of spikes, grains per spike, weight of spike and, length of peduncle when inoculated with the PGPR. IAA and ACC deaminase were produced by *P. fluorescens* strains (Azadikhah *et al.*, 2019). *P. fluorescens* showed positive nutrient dynamics in production of melons under saline stress (Martínez *et al.*, 2019; Safari *et al.*, 2018). Anumita *et al.*, (2018) studied halotolerant *Enterobacter* sp. strain P53 inoculated with rice seedlings. The bacteria disclosed ACC deaminase and produced IAA, HCN, siderophore and antioxidant activity under salt stress (Hussain *et al.*, 2018; Sarkar *et al.*, 2018a). Faiza *et al.*, (2018) showed the *S. fruticose* in saline conditions with various PGPRs. *S. jettensis* F-11, F-12, *S. arlettae* F-71, *B. marisflavi* F-87, *H. nanhaiensis* F-81, *Z. flava* F-9 and *E. mexicanum* F-35 were found to increase the root and shoot growth along with various plant growth enhancement factors. The mechanistic studies revealed the production of ACC deaminase, auxin, biofilm and antioxidant activity (Aslam and Ali, 2018).

• Volatile organic compounds (VOCs):

Reja *et al.*, (2019) investigated the effects of diverse levels of salt stress along with the introduction of bacterial growth stimulus on the amount of essential oil composition in *Rosmarinus officinalis*. The percentage of essential oils was directly proportional to the salinity either alone or with PGPR inoculation treatments till the saline

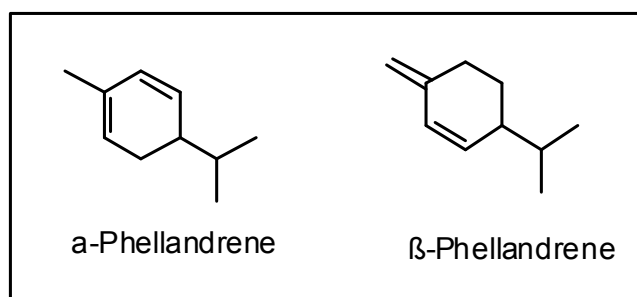


Fig. 5: Chemical structures of phellandrene.

condition of 10 g/L NaCl. Thereafter, it was moderated with additional upsurges in salt levels in treatments without using PGPR. The essential oil content was constant in treated with PGPR. Authors suggested that phellandrene (Fig. 5) was responsible for the activity (Bidgoli *et al.*, 2019).

• Exo-polysaccharides production:

Various bacterial isolates yielding exopolysaccharides have been characterized. Faranak *et al.*, (2019) studied *Citrobacter freundii* and SiO_2 nanoparticles on *Solanum lycopersicum* L. under saline stress. An increase in proline content, biomass, peroxidase and superoxide dismutase was established. Production of EPS lead to the increased development of biofilm which in turn increased the preservation of moisture and aggregation of soil (Isfahani *et al.*, 2019). In addition, Alla *et al.*, (2018) suggested that *Pseudomonas anguilliseptica* SAW 24 lead to the development of biofilm and production of exopolysaccharides in *Vicia faba* L. under saline stress. There was an increase in plant height, fresh weight and dry weight (Mohammed, 2018).

Meta-analysis studies

The meta-analysis by Pan *et al.* on 561 studies was conducted on salt-sensitive plants (SSP) and salt-tolerant plants (STP). There was an escalation in the levels of chlorophyll and carotenoid and photosynthetic rate in both SSP and STP under saline stress. This was related to the antioxidant effect of the PGPR under stress conditions. Further, the maintenance of ion homeostasis and osmotic balance were established. This was proposed by root structure modification and nutrient cycling acceleration, root nutrient absorption capacity elevation and firming Na^+ detoxification capacity have been seen to increase the biomass (Pan *et al.*, 2019).

Combination treatment

Aneela *et al.*, (2019) researched the combination of salicylic acid (SA) and PGPR for more growth of chickpea. Phosphorus and nitrogen content were escalated by this SA+PGPR combination. There were positive results in the shoot and root length and numbers

of nodules (Riaz *et al.*, 2019). Another study by Farhad *et al.* (2019), demonstrated the use of *Pseudomonas* sp. rhizobacteria in increasing the Mn^{2+} and Cl^- in *Pista ciavera* L. under saline stress. Pot experiment was carried out to check the IAA and siderophore production, phosphorus and zinc solubility, ACC deaminase activity and hydrogen cyanide (HCN). Under saline stress (2000 mg NaCl kg⁻¹), inoculation of pistachio seedlings with the *Pseudomonas* sp. improved the dry weight of shoot and root. Further uptake of Mn^{2+} was increased under the co-inoculation of the pistachio with the PGPR-Mn. PGPR-Mn effects were more pronounced and escalated the levels of organic matter bound- Mn^{2+} , carbonate bound- Mn^{2+} Water-soluble plus exchangeable- Mn^{2+} diethylenetriaminepentaacetic acid (Dtpa-extractable) Mn^{2+} and total chlorophyll content and decreasing the iron-manganese oxide-bound (FeMnOX) and residual Mn content etc. then Mn^{2+} alone (Atajan *et al.*, 2019).

In addition, Raheleh *et al.*, (2019) evaluated the effects of *Azospirillum lipoferum* and *Piriformospora indica* on *Sesamum indicum* L. under salt stress. Authors carried out the antioxidant enzyme assays, checked the lipid peroxidation and determined the content of total water, proline, chlorophyll, total phenols and flavonoids, sesamin and sesamol, oil, mineral nutrients etc. The results established under saline stress (120mM NaCl) indicated a significant increase in the SOD, CAT and APX activities when sesame was inoculated with single or combined PGPR's (*Azospirillum lipoferum* and *Piriformospora indica*). Proline content was more pronounced in AI-inoculation (120 mM NaCl; 311.66 μmg^{-1} FW) whereas electrolyte leakage was least in co-inoculated plants. *Azospirillum lipoferum* and *Piriformospora indica* lead to the 61.58% to 74.12% rise in reserved water content, maximum photochemical quantum yield of PSII (F_v/F_m) = 24.69% in 120mM NaCl condition. Further highest phenolic content (30.82 mg g⁻¹ DW), flavonoid content (10.75 mg g⁻¹ DW), sesamin (5327.17 ppm) and sesamol (3404.83 ppm) was found when inoculated under 80 mM NaCl in the presence of *Azospirillum lipoferum* and *Piriformospora indica* (Khademian *et al.*, 2019).

Sivagnanam *et al.*, (2019) demonstrated role of *Rhodotorula mucilaginosa* CAM4 in modifying aluminum, salinity and drought stress in *Lactuca sativa* growth. They formulated the powder of PGPR with combination of sawdust, molasses (5% w/w) and PEG (1% w/w). The activity was increased to about 1.34-3.57 fold for CAT, 1.58-5.16 fold FOR SOD and 1.61-4.78 fold for proline oxidase (POX) in comparison with both abiotic stressed and uninoculated control plants.

Further, in comparison to the uninoculated abiotic stressed plants, lettuce plants treated with different abiotic stresses formulated strain CAM4 had significantly decreased the proline concentration (50-61%) and MDA (Silambarasan *et al.*, 2019). Similarly, Sankalp *et al.*, (2019) (Misra *et al.*, 2019) demonstrated the role of *Jeotgalicoccus huakuii* NBRI 13E in the rhizosphere of tomato, maize and okra under salt stress. *Jeotgalicoccus huakuii* NBRI 13E had shown a positive activity for the carotenoid content, phosphorus solubilization, formation of biofilm, total chlorophyll content, EPS, IAA and ACC deaminase levels and total soluble sugar content etc. In comparison to the control PGPR inoculation offered an increase in shoot length, fresh weight/dry weight of plant and root length. The study concluded that combination of *Jeotgalicoccus huakuii* NBRI 13E and 50% NPK fertilizer under salt stress is an effective choice for improving crop productivity.

Rabba *et al.*, (2019) studied *Bacillus subtilis* with or without the mycorrhizal fungus *Rhizophagus intraradices* on *S. carnosa*. Production of IAA was established the reason behind the efficiency of *B. subtilis* in decreasing the salt induced stress. The combination improved the quality of soil and activities of soil enzymes such as urease, alkaline phosphatase, β -glucosidase and dehydrogenase and modulation of C:N:P stoichiometry (Hidri *et al.*, 2019).

Rhizobium strains had been found to produce ACC-deaminase, IAA and mineral-phosphate solubilizing in *Brassica napus* L under salt stress (Saghafi *et al.*, 2018). Further in a combination study, Josiane *et al.*, (2018) coinoculated maize with *Azospirillum brasilense* (Ab-V5 and Ab-V6) and *Rhizobium tropici* (CIAT 899) under saline stress. The combination of Ab-V6+CIAT 899 had been found to be most effective under saline stress, while Ab-V5 was unable to display the salt tolerance. Proline content and MDA was decreased whereas the antioxidant enzymes were upregulated. The mechanistic interventions revealed that the co-inoculation had a negative effect on *PR1*, *prp2*, *prp4*, *hsp70* and a positive effect on *APX1*, *CAT1*, *SOD2* and *SOD4* in leaves and *APX2* in the roots (Fukami *et al.*, 2018). In addition, Nasim and research group studied the PGPR's and kinetin on *Phaseolus mungo* under saline stress. There was an enhancement in LRWC, chlorophyll content, seed yield, shoot growth, biomass production and root growth of *Phaseolus mungo* treated with kinetin and/or H-PGPR under saline stress. Further electrolyte leakage was decreased under saline stress on the treatment of kinetin and/or H-PGPR (Yasin *et al.*, 2018b). The combination treatment of PGPR's with various agents are presented in fig. 6.

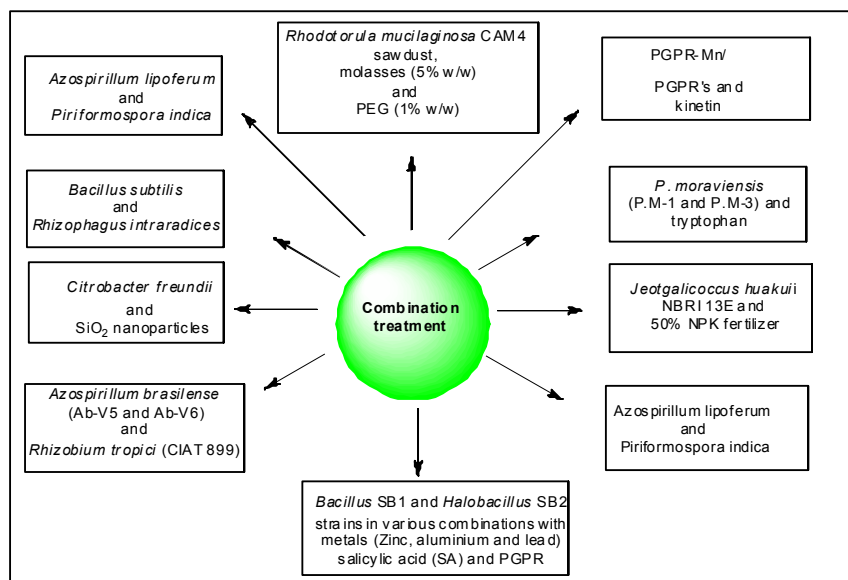


Fig. 6: Microbial consortia and combination treatment of plant growth-promoting rhizobacteria (PGPR) with various agents.

Mechanistic studies at molecular level

Maryam *et al.*, (2019) studied transcriptional responses of wheat roots inoculated with *Arthrobacter nitroguajacolicus* under salt stress. Authors established an increase in root and shoot mass and gain of iron, nitrogen, phosphorus and potassium. The studies revealed that there was a decrease in the sodium absorption and level of ethylene which was attributed to the increased ACC deaminase levels in wheat. Cytochrome P450s, ascorbate peroxidase (APX), Nicotianamine synthase gene, oligopeptide transporters (OPTs), ATP binding cassette (ABC) transporters, sugar/inositol transporter, ATPase, ion transporters were found to be upregulated (Safdarian *et al.*, 2019). *A. nitroguajacolicus* AK1 was also established to alleviate the salt stress by expressing *GmST1* and *GmLAX*₃ genes in soybean (Khan *et al.*, 2019a).

Szymańska *et al.*, (2019) studied the biochemical and growth parameters and expression levels of *RSH* genes ISE12 by *P. stutzeri* in *B. napus* under saline stress conditions. Further, high and low esterified homogalacturonan (HG) levels had also been explored. Biochemical (germination percentage and germination index) and growth parameters (leaf numbers, root length, chlorophyll content, hypocotyls length and stem length, fresh weight and dry weight) were escalated. *RSH1* and *RSH3* gene expression in *B. napus* organs were upregulated by the *P. stutzeri* via the antioxidant activity. There was an increase in lignin, suberin, glutathione and low methyl esterified HGs (Szymańska *et al.*, 2019). The research group also established bacterial microbiome of root-associated endophytes of *Salicornia europaea*

under saline stress. Bacteria belonging to the Fibrobacteres, Deltaproteobacteria, Acidobacteria, Verrucomicrobia and Caldithrix could be explored for the mitigation of saline stress (Szymańska *et al.*, 2018).

Tamoor *et al.*, (2019) researched IAA-Deficient Mutants of *Pseudomonas moraviensis* on wheat in saline conditions. They studied chlorophyll content, superoxide dismutase activity, peroxidase activity, transposon mutagenesis, salt tolerance potential, phytohormones, ABA and IAA. The results showed a decrease in pH (10%) in presence of *P. moraviensis* mutants (P.M-1 and P.M-3) under saline stress. In comparison to *P. moraviensis* (P.M-1 and P.M-3) alone, combination

of *P. moraviensis* (P.M-1 and P.M-3) and tryptophan displayed (compared to control) 17% decrease in sodium content, 47% increase in potassium content, 47-51 increase in plant height, 70% increase in proline content, 38% increase in seed number, 16% increase in seed weight. The combination also improved the organic matter in saline soil (Ul-Hassan and Bano, 2019).

Chakraborty *et al.*, (2019) put forth the insight into the biochemical retorts of wheat plants primed with *Ochrobactrum pseudogrignonense* under saline stress. The study revealed an increase in the peroxidase, glutathione reductase, ascorbate peroxidase and catalase under saline stress. Authors performed microarray investigation. *Ochrobactrum pseudogrignonense* lead to the downregulation of 282 genes (salt stress sensitive genes, ascorbate peroxidase and lipid transfer proteins etc.) and upregulation of 6022 genes (including peroxidase, chitinase, phenylalanine ammonia lyase, histone H2B and glucanase) under saline stress (200 mM NaCl) (Chakraborty *et al.*, 2019).

Yachana *et al.*, (2018) established green mechanism of PGPR-mediated stress handling. *Bacillus pumilus* and *Pseudomonas pseudoalcaligene* were explored in the defense-related pathogenesis-related protein induction. These PGPR's induced stress-related gene RAB18 and catalase for combating saline stress. Further authors concluded that these PGPR's are ideal for the regulation of sugar concentrations in plants as well as management of saline stress (Jha and Subramanian, 2018). Further, Ansari *et al.*, (2019) also established the positive role of *Bacillus pumilus* for the removal of saline stress in wheat. Authors found that *Bacillus pumilus* increased the

antioxidant potential of MDA, SOD, CAT and GR under saline conditions. The FAB10 strain also escalated the biofilm production, proline content, photosynthesis rate, efficiency of water use etc (Ansari *et al.*, 2019).

Firoz *et al.*, (2018) explored *Brevibacterium* sp. FAB3 in wheat under saline stress. The mechanistic interventions revealed the production of IAA, siderophore, solubilization of phosphate, HCN and ammonia (Ansari and Ahmad, 2018).

Chatterjee *et al.*, (2018) studied *Brevibacterium linens* RS16 in *Oryza sativa* under saline stress. The study showed the emission of foliage LOX, decanal, heptanal, nonanal, octanal, mono- and sesquiterpenes and volatile compounds, generation of ROS, reduced sodium ion uptake, escalation in leaf photochemical action and high level of Fv/Fm (Chatterjee *et al.*, 2018).

Nasim *et al.*, (2018) demonstrated the positive role of *Bacillus fortis* strain SSB21 in growth/generation of shoot and root length, chlorophyll content, protein content etc. of *Capsicum annum* L. under saline stress. On inoculation of plant and bacteria various stress related genes (CAPIP2, CaKR1, CaOSM1 and CACHi2) were upregulated. Further, the inoculation of *Bacillus fortis* strain SSB21 lead to an increase in proline biosynthesis, decrease in ROS, ethylene and lipid peroxidation (Yasin *et al.*, 2018a).

Al-sayed *et al.*, (2018) demonstrated the antioxidant potential of *Bacillus subtilis* (BERA 71) in chickpea plants under saline stress. *B. subtilis*-inoculated plants improved membrane stability under saline conditions via suppression of ROS generation and lipid peroxidation as well as the increased proline content (Abd_Allah *et al.*, 2018). Chakraborty *et al.*, (2018) studied *Bacillus safensis* (W10) to alleviate the saline stress in wheat plants. The genes for metallothionines, rubisco, expansins,

precursor of S-adenosylmethionine decarboxylase, Sulphur rich thionin-like proteins etc. were upregulated (Chakraborty *et al.*, 2018). Halophiles have been isolated from several habitats worldwide and genome of some halophiles like *Halobacillus trueperi* has been sequenced (Gupta *et al.*, 2019). The genome analysis can reveal the PGPR potential of the natural halophilic bacteria for application in agriculture of saline lands.

Conclusions

The increase in population has also amplified the demand of food and hence agriculture productivity. The saline stress has been one of the topmost problems to achieve the required production of agriculture crops. PGPR's confers a stable and reliable method to target this problem and production of necessary crop yield. Microbes that have PGPR activities can enhance plant growth, speed up seed germination, improve seedling emergence and protect plants from the deleterious effects of some environmental stresses including drought, salt and phytopathogens. Salt-tolerant rhizobacteria can play an important role in alleviating soil-salinity stress during plant growth. There has been extensive research in this field. *Pseudomonas* and *Bacillus* species have been the most explored class of PGPR's. Various others PGPR's have been explored (Fig. 7). PGPR has a great future prospective in the era of improving saline stress and agriculture productivity. There is a need of effective tools and techniques to identify the soil salinity and education to farmers about the PGPR's to improve the crop production. In general, the yield and growth of stress tolerant varieties of crops in presence of PGPR has been increased as compared to normal crop yield. Therefore, microbial inoculation to alleviate stresses and enhance yield in plants could be utilized as a cost effective environmental friendly option, potentially available in a

shorter time frame.

Acknowledgement:

The authors wish to express their warm and sincere thanks to Shoolini University, Solan, HP, India and CSSRI, Karnal, India for providing the necessary facilities and support for carrying out the research work.

Declarations

Conflicts of interest: None

Authors' contributions

Arti Sharma did the literature search and wrote the first draft; Kamal Dev,

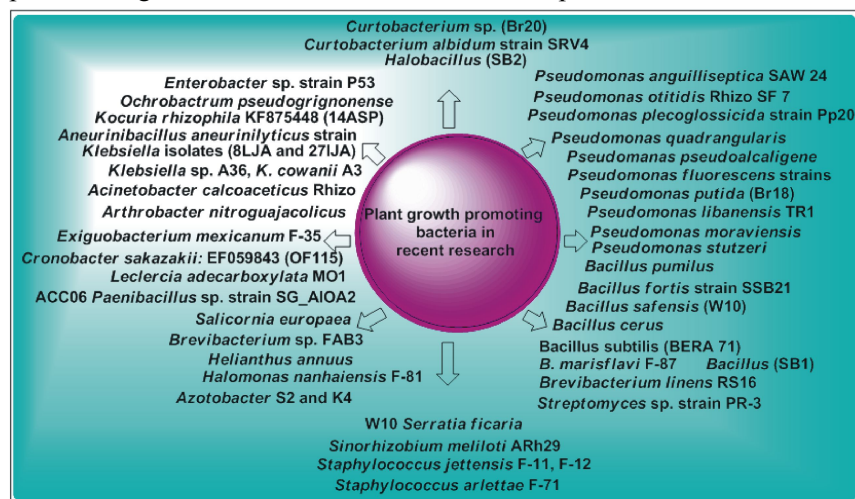


Fig. 7: Major group of Plant growth-promoting rhizobacteria (PGPR).

Madhu Choudhary and Anuradha Sourirajan conceived the study and edited and finalised the manuscript.

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