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Halotolerant PGPR: A hope for cultivation of saline soils

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ABSTRACT

Salt stress is one of the rapidly growing environmental stresses all over the world. Globally, 22% of the total cultivated and 33% of the total irrigated agricultural area is subjected to salt stress, which is increasing rapidly by an average of 10% per year. Due to this reason, 50% of cultivatable area will be salt-affected in coming years. On the other hand, demand for food is increasing with the rise in population. Salts have detrimental effects on plants such as damage to photosynthetic machinery, growth retardation and ultimately yield loss. However, the rhizosphere of plants harbors a diverse community of microbes known as halo-tolerant plant growth-promoting rhizobacteria (PGPR), which have the potential to cope with salinity problem. These PGPR assist plants to withstand the increased concentration of salts by the production of different organic and inorganic compounds such as Indole Acetic Acid (IAA), ethylene, 1-Amino Cyclopropane-1-Carboxylate (ACC) deaminase, volatile organic compounds (VOC), antioxidants etc.. The present review demonstrates the mechanisms of halo-tolerant PGPR that help plants to survive under saline conditions. We also highlighted some of the bacterial strains, which are successfully used in different forms on agriculturally important crops in salt affected soils. These halo-tolerant PGPR have the potential to work as defensive agents of plants by enhancing growth, productivity, tolerance and defense system under saline environments.

1. Soil salinity

The soil with extra salts affects the productivity of plant and is known as salt-affected soil (also called as soggy). In the root area, the saturation extract of saline soil has the electrical conductivity (ECe) more than 4 dS m^{-1} or 40 mM NaCl. The yield of many crops decreases at this electrical conductivity (Jamil et al., 2011). Two types of salinity occur in the soil; primary salinity occurs naturally when soil material is the main source of insoluble salts, whereas secondary salinity is caused by land and water assets that result from anthropogenic activities such as poor irrigation organization, unsatisfactory drainage, inappropriate cropping patterns, rotations, chemical contamination and vegetation sheath, which change the ecosystem of water balances (Singh, 2009). The key soluble salts in soil are cations: K^+, Na^+, Mg^{2+}, Ca^{2+}, and the anions Cl^-, HCO_3^-, and NO_3^-) (Rengasamy, 2006). Salts in saline water accumulate in soil gradually which decrease water level and increase concentration of soluble ions. Thus, salt level increase at the surface of soil resulting in the appearance of a salty soil. High concentration of salts in the soil also disturbs soil processes and the level of sodium at the interchange complex of the soil (sodicity) that affects the mechanical strength of soil. However, the harmful effects, of salts depend on many factors e.g. plant type, climatic conditions, and soil-water regulation. Due to an increase in the soil salinity, there is a great need to find the solution to this problem. The world population is increasing and world salt affected area will not be cultivable which would lead to famine conditions (Prins et al., 2011).

2. World salt-affected area

Predictably, salinity is one of the leading issues in the coming decades due to global increase in salt-affected area by 1 to 2% every

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Table 1
Salt-affected area of various worldwide regions.

Continents	Total area million ha	Saline soils million ha	Sodic soils million ha
Europe	2011	7	73
North America	1924	5	15
Latin America	2039	61	51
Asia, The Pacific and Australia	3107	195	249
Near East	1802	92	14
Others	1898	37	32
Total	12,781	397	434

FAO (2008).

year (Kasim et al., 2016). The salt-affected regions of the world and their magnitudes are presented in Table 1.

Salt stress negatively affects the farmers economically and socially. It has been estimated that $11 billion income of farmers might be reduced every year due to salinity issue. It is also estimated that the population will be 9.5 billion by 2050 (Singh, 2015) and to overcome food inadequacy, saline and barren lands will have to be used for cultivation purposes (Yan et al., 2015). Agricultural lands are the most desirable and suitable ones, however, the world authorities need to meet the demand of growing population otherwise, have to face the immense famine situation. It is reported that agricultural land will lose its capability of cultivation due to degradation by extensive use of man-made fertilizers, the salinity of soil, physical and chemical weathering (Ladeiro, 2012; Paul et al., 2003).

3. Impact of salinity on plant

Salinity affects the soil properties and equilibrium of the area and reduces the yield of crops, thus it plays role in reducing economic earnings. Different studies reported that salinity effects plants in many ways as reduced growth and development, reproductive development, germination, and vegetative growth, reduction in delayed spike, spikelet per spike, development and fertility, which leads to low grains (Munns and Rawson, 1999; Seckin et al., 2009). The harmful impact of salinity occurs in cell differentiation and cell cycle due to the decrease in the action of cyclins and expression of cyclin-dependent kinases, which causes the less cells growth in the meristem followed by the growth inhibition (Seckin et al., 2009). Salt affected soil causes ion toxicity, nutrient deficiency, oxidative and osmotic stress in plants, which restrict the uptake of water from soil. The elevated levels of Boron, chlorine, and sodium have particular harmful effects on plants. Several salts are present in nutrients of plant; their increased salt concentration in the soil can disturb the equilibrium of nutrient or affect the nutrient uptake by plant. Under salt stress, the metabolism and plant growth is badly affected by increased uptake of Na^+. Ion toxicity can change concentration of K^+ ions in chemical responses, which produce conformational variations in amino acids. High K^+ level is essential for tRNA binding with ribosomes and synthesis of amino acids (Zhu, 2003). The high accumulation of Na^+ in plants suppresses the photosynthesis and produces reactive oxygen species (ROS), which cause DNA damage, membrane injury, and protein degeneration (Islam et al., 2015). The cell walls with the increase of sodium triggers cell death and osmotic stress (Ashraf, 2004). Salinity also disturbs photosynthesis mostly by decrease in chlorophyll content, leaf area, stomatal conductance, and reduced efficiency of photosystem II efficiency. Disturbance in osmotic equilibrium causes damage of turgidity, cell dryness, and finally the death of cells. Osmotic stress and ion toxicity can result in metabolic inequality, and leads to oxidative stress. Plants possess different natural tolerance mechanisms to protect the damages due to the salt stress (Netondo et al., 2004).

4. Plant response against salt stress

In plants, different stress recognition and signaling pathways interact with one another in different ways by producing stress tolerance hormones, ion homeostasis, production of poly amines, activation and synthesis of antioxidant enzymes/compounds, and production of osmoprotectant (Groß et al., 2013). Several genes such as *SOS1* were associated with the abiotic stress response in tomato seedling (Huang et al., 2012; Koussevitzky et al., 2008). During salt stress, Ca^{2+} signaling pathway is triggered due to the expression of salt sensitive gene *(SOS1)* (Hrynkiewicz et al., 2015). These genes protect cells from damage by producing vital metabolic proteins. Downstream signaling of the stress pathway is identified by receptors of plasma membrane, which produces unique secondary messengers as inositol phosphates inducing oxidative bursts due to increased ROS level. The resulting *SOS1* genes help plant to survive during salt stress (Martínez-Atienza et al., 2007). Elevated ROS level damage lipids, nucleic acids and proteins (Halo et al., 2015). Plants respond to toxic level of ROS by producing antioxidants enzymes that leads to ROS detoxification and protect cells from its harmful effects by producing secondary metabolites like phenolic compounds. Ultimately, phenolics act as defensive agents under salt and drought stress (Miller et al., 2010). Several approaches have been established to reduce the damaging effects of salinity on plant both by genetic engineering and through the use of PGPR (Wang et al., 2003). The useful microorganisms inhabit the plant rhizosphere and stimulate plant growth via several indirect and direct mechanism (Upadhyay et al., 2012). Recent studies showed that microbial communities were also helpful to trigger the plant stress responsive genes and plants showed enhanced growth, yield, and development under stress conditions as shown as in Table 2.

5. Role of PGPR in salt stress tolerance

PGPR are rhizosphereic/endophytic bacteria that colonize root interior or exterior. According to previous reports, bacteria belong to different genera such as, *Microbacterium, Pantoea, Achromobacter, Rhizobium, Pseudomonas, Bacillus, Paenibacillus, Enterobacter, Burkholderia, Methylobacterium, Azospirillum,* and *Variovorax,* etc. provide tolerance to host plants during abiotic stresses (Akram et al., 2016; Shahid et al., 2018b). These microorganisms are useful in agricultural fields and can alleviate many abiotic stresses (Ashraf, 2004; Banaei-Asl et al., 2015; Wang et al., 2016). Several studies reported that stress tolerance is enhanced in plants by these microbes through different mechanisms as producing gibberellins, indole acetic acid, and some unidentified elements that results in increased root surface, root length area, root tips, and most importantly enhance nutrient content, thus improving the health of plant under salt stress (Shahid et al., 2018a, 2018b). Growth of different plants was improved by PGPR such as canola tomato, bean, lettuce and pepper in salt stress conditions. Some PGPR can produce cytokines, accumulate abscisic acid (ABA) and antioxidants that can detoxify ROS. Several parts of plant are ethylene-dependent, thus production of ethylene is important for post-transcriptional and transcriptional modifications that are regulated during salinity stress (Barassi et al., 2006). Under stress situations, the ethylene hormone also controls plant homoeostasis (Tewari and Arora, 2014). ACC deaminase produced by bacteria degrades plant ACC for acquiring energy and nitrogen. Moreover, it also decreases the harmful impact of ethylene, by enhancing stress tolerance and promoting growth of plant. Bacteria also produce *exo*-poly saccharides (EPS), which show the mitigating effects against salinity and water pressure to enhance the structure of soil. Cations containing Na^+ bind to EPS thus Na^+ cations are inaccessi-

Table 2
Role of PGPR as salt tolerance in recent research.

Strain of PGPRs	Crop	Improved characters of crop	Reference
Achromobacter sp.	*Lycopersicon esculentum*	Reduce ethylene level	Mayak et al. (2004)
Acinetobacter sp.	*Cucumis sativus*	Reduce ethylene content	Kang et al. (2014)
Aeromonas sp.	*Triticum aestivum*	Exopolysaccharide production	Ashraf et al. (2004)
Arthrobacter sp.	*Pisum sativum, Triticum, aestivum* L	Improved plant growth due to increased nutrient up take	Barnawal et al. (2014); Upadhyay et al. (2011); Tiwari et al. (2011)
Azospirillum sp.	*Helianthus Annuus* L, *Zea mays*	Improved chlorophyll content	Naz and Bano (2015); Hamdia et al. (2004)
Azotobacter sp.	*Zea mays*	Improved nutrition	Rojas-Tapias et al. (2012)
Bacillus sp.	*Arabidopsis thaliana, Solanum lycopersicum, Cucumis sativus, Glycine* max, *Vigna radiata* L, *Puccinellia tenuiflora, Zea mays, Triticum, aestivum* L, *Oryza sativa, Codonopsis pilosula*	Improved plant growth by ACC deaminase activity	Ashraf et al. (2004); Cho et al. (2008); Damodaran et al. (2013); Nadeem et al. (2016a); Niu et al. (2016); Pourbabaei et al. (2016); Li and Jiang (2017); Ramadoss et al. (2013); Han et al. (2017); Upadhyay et al. (2011); Kumari et al. (2015); Patel et al. (2015); Khan et al. (2017); Jha et al. (2011)
Brachybacterium sp.	*Arachis hypogaea* L.	High K^+ content	Shukla et al. (2012)
Brevibacterium sp.	*Arachis hypogaea* L.	High K^+ content	Shukla et al. (2012)
Burkholdera sp.	*Cucumis sativus*	Increase water and chlorophyll content	Kang et al. (2014)
Curtobacterium sp.	*Hordeum vulgare* L.	Production of proline	Cardinale et al. (2015)
Enterobacter sp.	*Oryza sativa, Brassica napus, Triticum aestivum, Solanum lycopersicum, Zea mays, Arabidopsis thaliana*	Reduced ethylene production	Nadeem et al. (2009), Nadeem et al. (2013), Kim et al. (2014), Sarkar et al. (2017)
Enterococcus sp.	*Vigna radiata* L.	Salt tolerance due to less uptake of sodium	Panwar et al. (2016)
Exiguobacterium sp.	*Mentha arvensis*	Production of exopolysaccharides	Bharti et al. (2014)
Geobacillus sp.	*Zea mays*	Increased proline content and photosynthetic	Abdelkader and Esawy (2011)
Haererohalobacter sp.	*Arachis hypogaea* L.	High K^+ content	Shukla et al. (2012)
Halo bacillus sp.	*Sesuvium portulacastrum*	Production of ammonia and HCN	Desale et al. (2014)
Hartmannibacter sp.	*Hordeum vulgare* L	Exopolysaccharide production	Suarez et al. (2015)
Klebsiella sp.	*Triticum aestivum, Avena sativa*	Increase K^+ content and proline level	Singh et al. (2015); Sapre et al. (2018)
Kocuria sp.	*Fragaria ananassa*	Maintenance of phosphate	Karlidag et al. (2013)
Microbacterium sp.	*Triticum aestivum*	High K^+ content	Ashraf et al. (2004)
Micrococcus sp.	*Arabidopsis thaliana and Oryza sativa*	Production of IAA and siderophore	Sukweenadhi et al. (2015)
Oceanobacillus sp.	*Lens esculenta*	Production of exopolysaccharides	Qurashi and Sabri (2011)
Ochrobactrum sp.	*Arachis hypogaea* L	Production of IAA and ACC deaminase	Paulucci et al. (2015)
Pantoea sp.	*Vigna radiata* L.	Salt tolerance by improved ACC deaminase activity	Panwar et al. (2016)
Pseudomonas sp.	*Arachis hypogaea, Zea-mays, Brassica napus, Helianthus annuus, Cucumis sativus, Glycyrrhiza uralensis, Galega officinalis* L., *Glycine* max, *Arachis hypogaea, Cappisum annuum, Silybum marianum, Triticum, aestivum* L, *Vigna radiata, Cucumis sativus, Solanum lycopersicum, Gossypium hirsutum*	Improved plant growth due to enhance proline, IAA, and EPS content production	Chatterjee et al. (2017); Zerrouk et al. (2016); Nadeem et al. (2016b); Egamberdieva et al. (2013a); Niu et al. (2016); Egamberdieva et al. (2013b); Nadeem et al. (2009); Egamberdieva (2012); Kohler et al. (2009); Kumari et al. (2015); Jha et al. (2011); Yao et al. (2010)
Raoultella sp.	*Gossypium annuum*	ACC deaminase activity	Wu et al. (2012)
Rhizobium sp.	*Pisum sativum, Vigna radiate, Zea mays*	Increased chlorophyll + photosynthesis rate	Ahmad et al. (2014); Barnawal et al. (2014); Bano and Fatima (2009); Cardinale et al. (2015)
Serratia sp.	*Triticum aestivum* L	Production of exopolysaccharides	Singh and Jha (2016); Nadeem et al. (2013)
Sino- rhizobium sp.	*Medicago cilitaris*	Improve growth due to high proline content	Salah et al. (2013)
Sphingomonas sp.	*Solanum lycopersicum*	Production of exopolysaccharides	Halo et al. (2015)
Streptomyces sp.	*Limonium sinense, Solanum lycopersicum,*	Production of proline	Palaniyandi et al. (2014); Qin et al. (2017)
Variovorax sp.	*Pisum sativum*	Production of ACC deaminase	Wang et al. (2016)

ble to plants in saline environment (Timmusk et al., 2014; Tewari and Arora, 2014). Expression of *proBA* gene in *Arabidopsis thaliana* increased concentration of free proline which enhance osmotic tolerance of these genetically modified plants (Chen et al., 2007). Inoculation of *Pseudomonas* and *Rhizobium* in *Zea mays* increases proline concentration, reduce electrolyte leakage, and selection of K^+ ions enhance the salt tolerance (Vardharajula et al., 2011). Inoculations of specific PGPR help to encourage salt stress tolerance of plants via induced systemic tolerance (IST) which causes many functional and biochemical changes (Yang et al., 2009).

5.1. Mechanisms of PGPR to tolerate salt stress

The PGPR have direct (phosphate solubilization, nitrogen fixation, IAA synthesis etc.) and indirect (antioxidant defense, VOC, EPS, osmotic balance) mechanisms for improving plant growth and enhancing tolerance against salinity stress. Many bacterial factors are involved in enhancing IST such as IAA synthesis, activity of ACC deaminase, exopolysaccharide production, VOCs and siderophore production (Yang et al., 2009). Current review focuses on indirect mechanism induced by halo-tolerant PGPR to induce tolerance against salt stress.

5.1.1. Antioxidants

Normally, ROS is produced in less quantity during cellular metabolism of plants. However, under stress conditions, ROS increases which changes redox state, DNA damage, denature membrane bounded proteins, reduce membrane fluidity, changes the protein formation, damage the enzymatic actions and homeostasis of cell, which can damage the cell and finally cell death (Halo et al., 2015). During salt stress lipids are main targets of ROS that affects phospholipids (poly-unsaturated fatty acids) of membrane and start peroxidation of lipid (Miller et al., 2010). Enzymatic antioxidants as mono dehydroascorbate reductase, superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and non-enzymatic antioxidants as, tocopherols, ascorbate, cysteine, and glutathione are involved in degrading ROS and promote tolerance against oxidative stress (Kim et al., 2014). Various PGPR are reported to tolerate the oxidative stress with the help of antioxidants enzymes. APX activities increased under salt stress in inoculated tomato seedling by *Enterobacter* spp. (Sandhya et al., 2010). Inoculation of PGPRs to gladiolus plant showed higher the CAT, and SOD as compared to control (Damodaran et al., 2013). However, Inoculation gladiolus plant with PGPRs showed higher CAT, and SOD as compared to control (Kim et al., 2014).

5.1.2. EPS

Rhizobacteria produce EPS, which are in the form of hetro or homo polysaccharides that bind to the surface of the cell like a capsule and form a biofilm (Upadhyay et al., 2011). Polysaccharide composition differs between different species but some common monomers contain mannose, glucose, and galactose. Amino sugars (N-acetylamino sugars), neutral sugars (galacturonic), uronic acids, (fucose and rhamnose), pyruvateketals, and ester-linked substituents are EPS constituents. The PGPR inoculated plants have increased potential to ameliorate the oxidative stress (Miller et al., 2010). PGPR that produce EPS show significant role in growth of plant during salinity stress conditions by forming hydrophilic biofilms (Rossi and De Philippis, 2015). Rhizobacteria producing EPS have potential to fight against salt stress by making rhizosheaths around the roots of plants by attaching the EPS with Na^+ ions. Attachment of EPS to Na^+ ions reduces the toxicity of Na^+ making it unavailable for plants. It was reported that inoculation of *Bacillus subtilis* to *Arabidopsis thaliana* reduces the influx of Na^+ through down regulating the expression of HKT1/K^+ transporter (Zhang et al., 2008). In another study, inoculation of *Pseudomonas aeruginosa* to *Helianthus annuus* reduced the salt stress by producing the EPS, thus resulting in enhanced yield, development, and growth (Tewari and Arora, 2014).

5.1.3. VOCs

Rhizobacteria-oriented VOCs are lipophilic fluids having high vapor pressures. They are species-specific and communicate between organisms through cell signaling in order to promote growth. The VOCs promote biosynthesis of choline and glycine betaine, which improves plant tolerance against osmotic pressure. The VOCs of *Bacillus subtilis* trigger tissue specific gene regulation

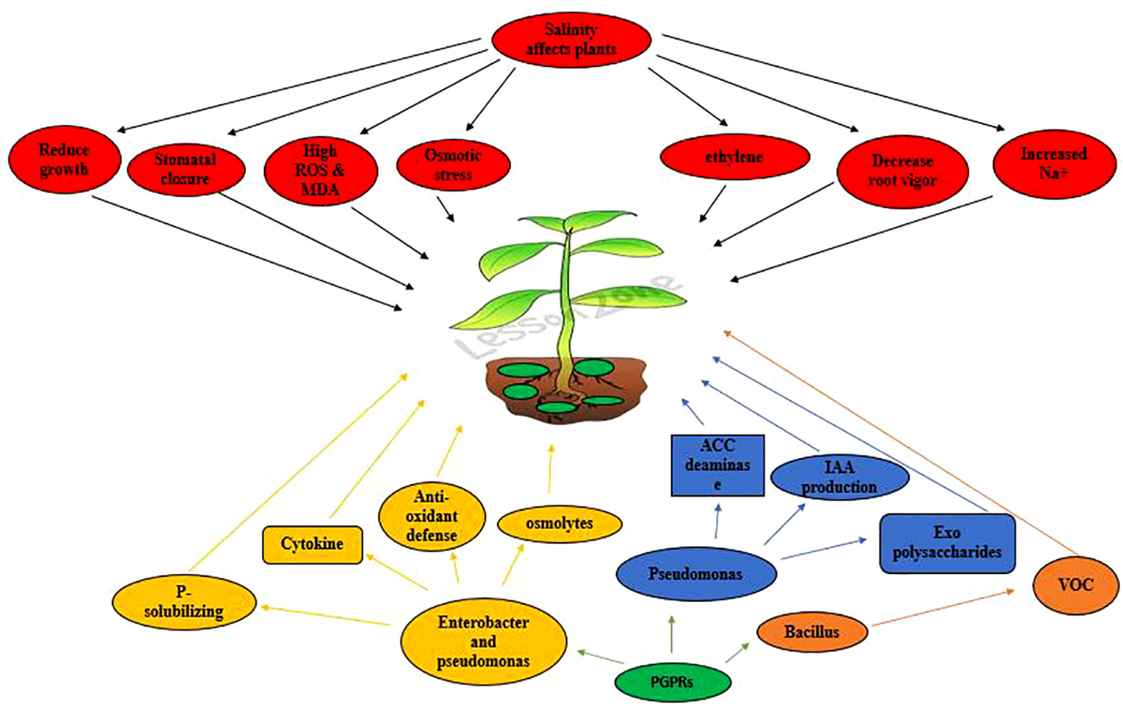

Fig. 1. Plants are affected due to salt stress in many ways as increased uptake of Na^+, high production of ROS, MDA and high ethylene level, however different PGPRs protect the plant by various mechanism such as IAA (indole acetic acid), VOC (volatile organic compounds), HKT1(high affinity K+ transporter), and antioxidant defense system [modified from (Kaushal and Wani, 2016)].

of HKT1/K^+ transporter that inhibits sodium ions influx through roots in order to eliminate the salt stress (Zhang et al., 2008). The VOCs produced by *Bacillus subtilis* encourage the synthesis of glycine betaine and induce less uptake of Na^+ through roots and also improve nutrients transport from root towards shoot during salt stress. The level of VOCs is low in plants and it is higher under stress conditions. The high level of VOCs is a sign to activate self-protective response against salt stress (Timmusk et al., 2014).

5.1.4. Osmotic adjustment

Increase of compatible solutes to retain the cell turgidity within borderline that is essential for regular cell functions is called osmotic adjustment. It is main cellular machinery in plants that reduces osmotic stress produced due to salt stress (Gill and Tuteja, 2010). In salt stress, PGPR produce compatible osmolytes to help plants promote their growth. During stress condition, proline and glycine betaine are accumulated in plants, however, plants lack the production of organic osmolytes like trehalose. Proline is the key of osmolytes, that formed in plant by the hydrolysis of proteins to reduce osmotic stress (Krasensky and Jonak, 2012). Under salt stress conditions proline play multifunctional role like proteins maintenance, regulating cytosolic acidity, decrease lipid peroxidation and ROS scavenging. Rhizobacteria inoculation in plants showed improved proline levels under salt stress. Inoculation of *ProBA* gene to *A. thaliana* led to regulated by 35 S promoter stronger of cauliflower mosaic virus and produce proline (Wang et al., 2016). It is involved in the osmotolerance of transgenic plants, synthesis of trehalose which protect the plants when inoculated with PGPR and maintains proteins and membrane integrity (Chen et al., 2007). Moreover, trehalose also acts as osmoprotectant under stress conditions like osmotic stress, drought, high salt stress and low temperature (Liu et al., 2016). The quaternary compound glycine betaine, found in different animals, microorganisms and plants, is involved in inducing tolerance against stressful conditions (Cho et al., 2008). Glycine betaine is not only protecting the plants against many stresses but also protects several stress-relieving enzymes by forming proteins quaternary structure and other macromolecules (Ahmad et al., 2013). Several salt tolerant bacteria have enormous number of genes to survive under salt stress including sodium/hydrogen (Na^+/H^+) antiporter genes etc. These genes are involved in maintaining the cells by Na^+ detoxification, formation of Na^+ electrochemical gradient, adjustment of cell volume, and homeostasis of cellular pH. The *Escherichia coli* and several *Enterobacter* spp. have Na^+/H^+ antiporter gene that plays role the ion homeostasis mechanism with the help of *nhaA* gene. *NhaA* is necessary for adaptation of plants in high salinity due to its distinctive capacity for 'sensing' the environmental signals given by Na^+/ H^+ and maintains cellular homeostasis. *NhaA* gene is identified in *Enterobacter ludwigii* (Padan, 2008), to tolerate the salt stress as shown in Fig. 1 (Padan, 2008).

6. Conclusion

Under saline conditions, soil microflora and/or halo-tolerant PGPR, play a vital role in the amelioration of physiological abnormalities induced by salts in plants. Halotolerant PGPR are involved in inducing the salt tolerance in various plants to help them survive under saline conditions and followed by improvement in their morphological parameters. These halo-tolerant PGPR are involved in physiological aid of plants through the production of antioxidants, VOC, EPS and osmotic adjustment in plants. Moreover, different novel genes of plants as *SOS1* are regulated by PGPR which activates the plant defense system against salinity. *ProBA* gene in *Bacillus subtilis* and *NhaA* gene in *Enterobacte*r *ludwigii* are identified as salt tolerant thus, can be used to produce transgenic plants which might be tolerant against salt stress using advance biotechnological techniques. Halo-tolerant PGPR are natural microflora that enhances plant growth and crops productivity but all of these are not explored yet. In future, the halotolerant PGPR can be utilized as biofertilizer to ameliorate salt stress and increase crop production in an economically sustainable manner.

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