Climate Change and Salinity Effects on Crops and Chemical Communication Between Plants and Plant Growth-Promoting Microorganisms Under Stress

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During the last two decades the world has experienced an abrupt change in climate. Both natural and artificial factors are climate change drivers, although the effect of natural factors are lesser than the anthropogenic drivers. These factors have changed the pattern of precipitation resulting in a rise in sea levels, changes in evapotranspiration, occurrence of flood overwintering of pathogens, increased resistance of pests and parasites, and reduced productivity of plants. Although excess CO_2 promotes growth of C_3 plants, high temperatures reduce the yield of important agricultural crops due to high evapotranspiration. These two factors have an impact on soil salinization and agriculture production, leading to the issue of water and food security. Farmers have adopted different strategies to cope with agriculture production in saline and saline sodic soil. Recently the inoculation of halotolerant plant growth promoting rhizobacteria (PGPR) in saline fields is an environmentally friendly and sustainable approach to overcome salinity and promote crop growth and yield in saline and saline sodic soil. These halotolerant bacteria synthesize certain metabolites which help crops in adopting a saline condition and promote their growth without any negative effects. There is a complex interkingdom signaling between host and microbes for mutual interaction, which is also influenced by environmental factors. For mutual survival, nature induces a strong positive relationship between host and microbes in the rhizosphere. Commercialization of such PGPR in the form of biofertilizers, biostimulants, and biopower are needed to build climate resilience in agriculture. The production of phytohormones, particularly auxins, have been demonstrated by PGPR, even the pathogenic bacteria and fungi which also modulate the endogenous level of auxins in plants, subsequently enhancing plant resistance to various stresses. The present review focuses on plant-microbe communication and elaborates on their role in plant tolerance under changing climatic conditions.

Keywords: climate change, salinity, halotolerant PGPR, biofertilizers, stress tolerance

INTRODUCTION

Drivers of Climate Change

Variations in the atmospheric conditions of a particular region for a long period is known as climate and changes in the atmospheric variables beyond the average value is known as climate change. Different forces are responsible for variations in atmospheric variables. They are broadly categorized into two main groups: anthropogenic and natural drivers. Anthropogenic drivers are well-mixed greenhouse gases (WMGHGs), i.e., CO_2, CH_4, and nitrous oxide (N_2O), whereas solar irradiance and earth orbit, volcanic eruption, and chemical weathering of rocks are examples of natural climate drivers. The greenhouse gasses cause changes in climate by trapping heat, initiating wildfires, and disrupting food supply (Cassia et al., 2018). Volcanic eruptions cause a reduction in the amount of solar radiation, decreasing the temperature in the troposphere and changing atmospheric circulation patterns. Similarly, the chemical weathering of rocks also caused climate cooling by consumption of CO_2 (Huh, 2003). The effects of natural drivers on climate change are relatively less compared to anthropogenic impacts (Nelson et al., 2006; Rosa et al., 2015; Myhre et al., 2017). Synthetic fertilizers used in agriculture are responsible for the production of about 80% growth rate of N_2O (Ciais et al., 2014). Global rice production is responsible for >10% of total CH_4 emission (Smartt et al., 2016).

Variables of Climate Change

The bioindustry of agriculture is greatly influenced by temperature, precipitation, and sunlight. These elements are vulnerable to climate change. A significant increase in global mean temperature (GMT) is induced by artificial drivers as compared to natural drivers of climate (Myhre et al., 2017). It influences precipitation patterns which might lead to drought or inundation. An increase in temperature and decrease in precipitation would affect soil properties (Gelybó et al., 2018). It also affects soil organic carbon as a decrease in water ratio lowers the decomposition process and mineralization of different organic compounds (Karmakar et al., 2016; Onwuka and Mang, 2018). Change in soil temperature also influences soil moisture content, water holding capacity, and soil particle size. Increased soil surface temperature also increases the rate of evaporation and restricts the movement of water in soil profile (Onwuka and Mang, 2018). One study has shown that clay size and organic matter, which decrease in response to increased soil temperature, lead to reduced cation exchange capacity (CEC) (Certini, 2005). Reduced productivity of livestock, horticulture, and cultivated crops is directly related to broad scale alterations in climatic conditions (Malla, 2008).

## Negative Impacts of Climate Change on Agricultural Productivity

Climate change and food security are two main issues of the 21st century. The world population is expected to reach 9 billion by the end of 2050, and food requirements are expected to escalate by 85% (FAO, 2017). The agriculture sector is highly threatened by the increased frequency of droughts, heavy rainfall, fluctuations in temperature, salinity, and insect pest attacks on major food crops (Dhankher and Foyer, 2018; Hussain et al., 2019). The FAO declared that 20% of total emissions of GHGs were from agriculture and land use practices. Changes in precipitation patterns, increased frequency of dry spells and drought, rising temperatures, rising sea levels, and temperature variability have negative impacts on agriculture production (**Figure 1**). Zhao et al. (2017) constructed different simulation models to investigate the effect of increased temperature on yield of four crops by analyzing yield data from 46 research articles and 48 sites on a global scale. He concluded that for each degree increase in global mean temperature (GMT), the production of wheat has been predicted to reduce by 6.0%, rice by 3.2%, maize by 7.4%, and soybean by 3.1% around the world. Depending on geographical regions, the effect of temperature may be positive or negative. In general, a rise in temperature has caused a shift in the phenological development of crops (Teller, 2016), lower water use and nitrogen use efficiency (Ullah et al., 2019), shortening of vegetative and reproductive growth phases of plants (Wang et al., 2018), and decrease in the number of grains and grain-filling duration (Lin et al., 2017). The proliferation of insects and pests at high rates which attack major crops are indirect effects of climate change (Dhankher and Foyer, 2018). The largest grain producers of the world viz. China, the US, and France are facing major infestations of crop pests and consequent yield losses (Shrestha, 2019). This is because increased temperatures and precipitation promote the growth and spread of many pest species.

Climate Change and Salinity

Soil salinity is one of the impacts of climate change in coastal agriculture land, as rises in sea levels has increased salinity from 1 to 33% over 25 consecutive years (Rahman et al., 2018). Sea level rise is associated with the increase in global warming and occurs due to the melting of glaciers and ice sheets as well as the thermal expansion of sea water. Bhuiyan and Dutta (2012) demonstrated a comprehensive understanding of the possible effects of sea level rise with the aid of a hydrodynamic model. Sea level rise includes flooding and salinization and has implications for water resources. Rising sea levels increase the salinity of both surface water and ground water through saltwater intrusion.

Salinity is more evident in semi-arid, coastal agriculture lands, and particularly in arid regions of the world (Kasim et al., 2013; Qadir et al., 2014; Hashem et al., 2018). Changes in weather patterns have resulted in the frequency of recurrent drought or rain falling above the average value for more than a decade (Ayanlade et al., 2018). The upward movement of water in areas with shallow water tables and coastal areas with sea water intrusion resulted in root zone salinity. Changes in precipitation and temperature have a greater influence on soil salinity. In one study conducted by Bannari and Al-Ali (2020), it has been reported that the long-term effects of increased temperatures and decreased precipitation for 30 years showed a positive correlation with increased soil salinity in arid landscape due to less over leaching of salt in the soil as determined by Landsat sensor data including Thematic Mapper (TM), Thematic Mapper Plus (ETM+), and Operational Land Imager (OLI). In coastal agriculture lands, the salinity has increased from 1 to 33% in the last 25 years (Rahman et al., 2018).

FIGURE 1 | Impact of climate change on agriculture.
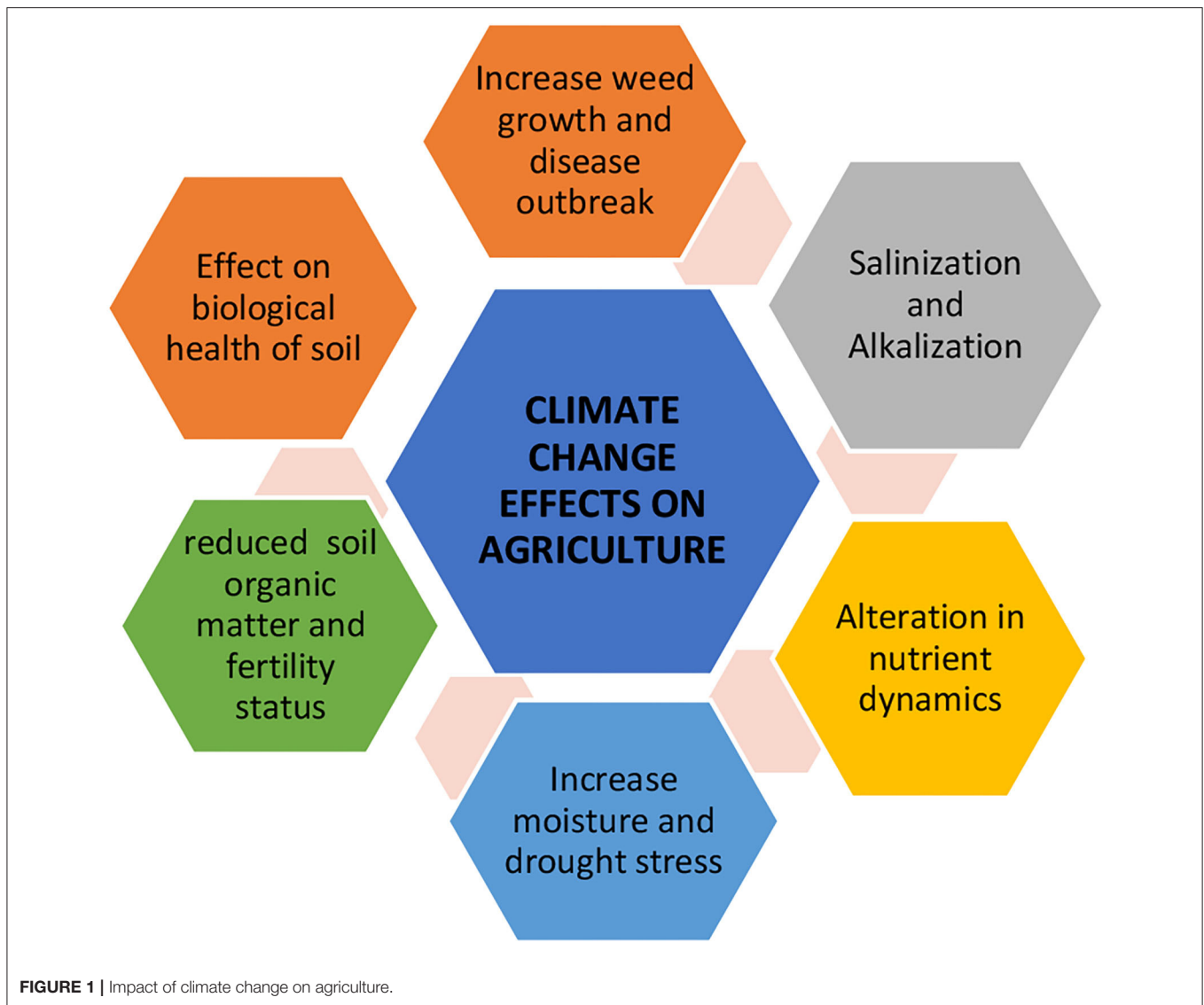
On a global level, more than 831 Mha of agriculture land is salt-affected (FAO, 2008); salinity affected 397 M ha, while sodicity affected up to 434 M ha land (Martinez-Beltran, 2005; Setia et al., 2013). Out of the total cultivated and irrigated agriculture land, 50% is affected by high salinity on a global level (Zhu, 2001; Gengmao et al., 2015). Irrigation with saline water, low precipitation, and high evapotranspiration are key factors that cause salinization at a rate of 10% annually to agricultural lands. At this rate more than 50% of arable land would be salinized by 2050 (Jamil et al., 2011). Expansion of salt-affected arable lands has emerged as a major threat toward world food security. About 6% of the cultivated area is destroyed by soil salinization with a continued addition of 1–2% every year around the globe, causing significant yield losses of staple grain crops like maize, rice, and wheat (Munns and Tester, 2008). High rates of evapo-transpiration results in accumulation of salt on the soil surface (Ashraf et al., 2002; Munns, 2002). Most of the underground water used for crops in such conditions

become brackish and contains a high content of soluble salt ions, such as Na^+ and Cl^-, and lower quantities of K^+, Ca^{2+}, and NO^{-3} (Abro et al., 2007; Munns and Tester, 2008). The presence of these ions results in hyper ionic salt stress, which induces metabolic impairment and oxidative stress through the generation of reactive oxygen species (ROS), thus adversely impacting the yield of crops (El-Hendawy et al., 2005; Petrov et al., 2015; Caverzan et al., 2016).

Negative Impacts of Salinity on Crop Physiology

Salinity exerts its detrimental effect on plants by two mechanisms: osmotic stress and ion toxicity. The first effect is short term and occurs due to the uptake of Na^+ and Cl^- which reduce osmotic potential between root and soil solution and infiltrate water availability (Abbasi et al., 2016). Secondly, high concentrations of Na^+, Cl^-, or SO_4^{2-} induce ion toxicity that affect nutrient uptake (Tavakkoli et al., 2011). Sodium chloride (NaCl) toxicity

is directly related to electrical conductivity (EC), which is an indicator of plant tolerance to salt stress (Isla and Aragüés, 2010). Crop tolerance decreases beyond 2 dSm^{-1}, while some plants grow well even at 8 dSm^{-1}. Beyond this limit, growth and yield are negatively impacted. The adverse effects of salinity on crop morphology, physiology, and yield are listed in **Figure 2**. Seeds sown in saline conditions are poorly germinated (Ullah and Bano, 2019). Salinity decreases the endogenous level of phytohormones and inhibits seedling establishment (Egamberdieva and Kucharova, 2009). If seeded in the first phase of salinity, shoot growth will be affected in later stages (El Sayed, 2011; Wakeel et al., 2011). Even if seedlings are vigorous and maintain normal growth in the second phase of salinity, yield will be affected at the end. Salinity causes various physiological impairments in plants; due to less stomatal conductivity, C-fixation capacity becomes limited, disturbing the catalytic activities of enzymes that fix C and destroy photosynthetic pigments (Omoto et al., 2012). A significant decrease in shoot and root biomass has been recorded in plants grown in saline soil (Kalhoro et al., 2016; Genc et al., 2019).

Studies showed that salinity (10 mM NaCl) reduced the yield of *Triticum aestivum* up to 65% (Khan et al., 2004; Shafi et al., 2010). Elevated levels of salt in the root medium reduced the uptake of K, Ca, and Mg (Keutgen and Pawelzi, 2009; Hussin et al., 2013), leading to disturbances in stomatal conductance and transpiration rate (Sumer, 2004). Iron (Fe) is an important metal activator (co-factor) of different antioxidant enzymes (Kumar et al., 2010; Sharma et al., 2012), which helps in regulating life sustaining processes in plants, i.e., photosynthesis and chloroplast biosynthesis. Rabhi et al. (2008) reported that saline sodic soil is deficient in Fe. Plants grown in such soil showed interveinal chlorosis and a declined yield (Lan et al., 2011). Chloride ion (Cl^-) is a predominant ion in saline environments and the uptake of N is indirectly correlated to it. Salinity-induced increased Cl uptake is often associated with decreased uptake of nitrate by crops (Wang et al., 2012; Sadale and Karadge, 2013; Yu et al., 2016; Hasana and Mayake, 2017; Kanagaraj and Desingh, 2017).

Oxidative stress induced by salinity as secondary stress leads to the production of ROS, i.e., O^{-2}, OH, and H_2O_2 (Apel and Hirt, 2004; Voothuluru and Sharp, 2012; Chawla et al., 2013). As a toxic byproduct of aerobic metabolism, ROS are primarily found in the chloroplast, mitochondria, and peroxisome. Their enhanced production cause lipid peroxidation that affects photosynthesis and membrane permeability, damages nucleic acids, inhibits enzymes, and activates programmed cell death (Apel and Hirt, 2004; Tanou et al., 2009; Mishra et al., 2011; Srivastava and Dubey, 2011). *Brassica napus* and *Triticum aestivum* grown in saline conditions experienced poor growth and yield due to elevated levels of saline water (Hasanuzzaman et al., 2011a,b).

STRATEGIES TO COPE WITH SALINITY STRESS UNDER CHANGING CLIMATE

Physical Methods

Some physical methods to reclaim salt-affected soil include scraping, deep plowing, deep tillage, sub soiling, sanding, horizon mixing, profile inversion, flushing, and leaching. Scraping is
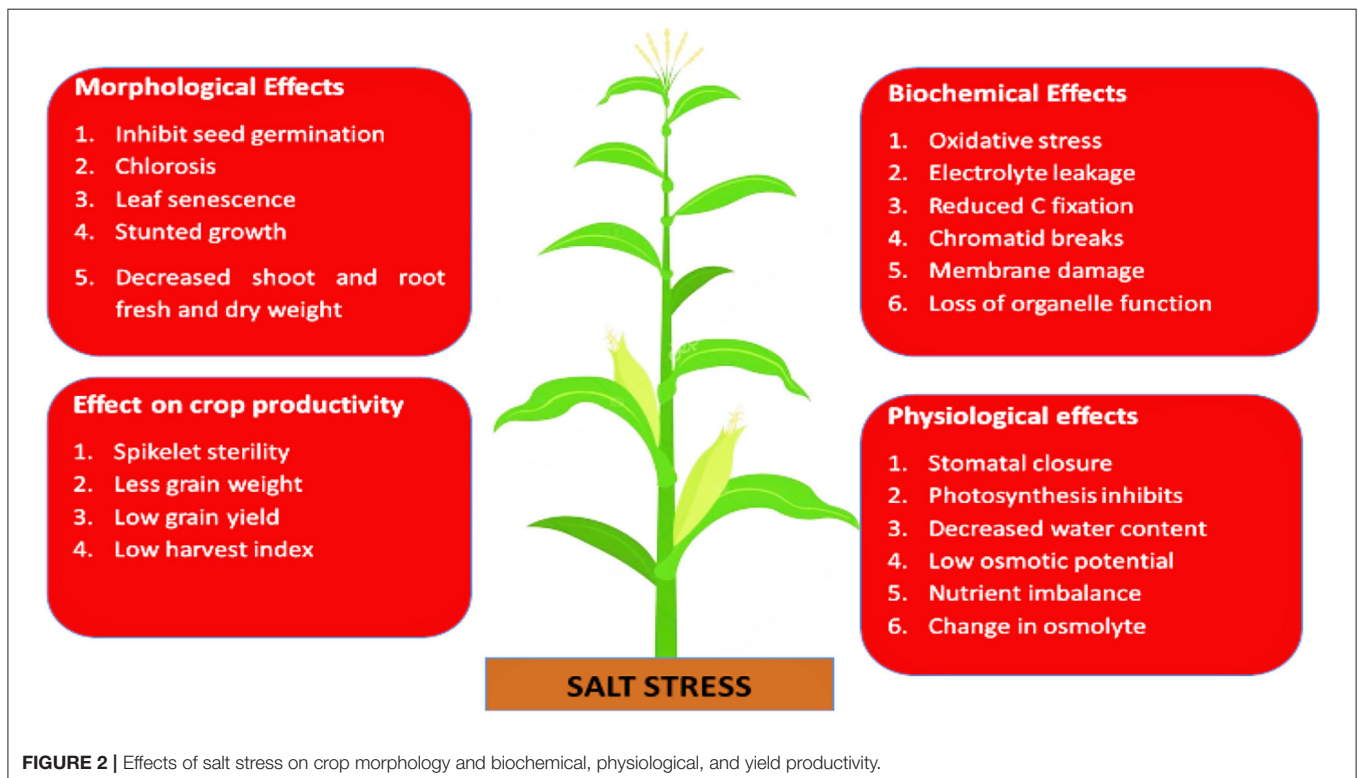

FIGURE 2 | Effects of salt stress on crop morphology and biochemical, physiological, and yield productivity.

used by farmers to mechanically remove salt from soil surface; however, it is a temporary measure to improve plant growth, and the ultimate disposal of salt remains a major problem. Flushing is used to desalinate soil with surface salt crusts. This method can flush small amounts of salt but has little practical significance. The most common method to reclaim saline soil involves leaching, in which good quality water is supplied to surface soil to leach salt levels (Ghafoor et al., 2012; Yan and Marschner, 2013). The leached salt is then removed with an adequate drainage system.

Chemical Methods
Reclamation by Inorganic Amendment
Saline sodic soil can be reclaimed by the application of Ca^{2+}-containing chemicals which replace Na^+ at soil exchangeable sites, followed by leaching with good quality water supply (Gupta and Abrol, 1990). Application of gypsum in soil with low concentrations of carbonate has been extensively studied (Horney et al., 2005; Gharaibeh et al., 2011). It is commonly used to supply Ca^{2+}. However, for soil containing high carbonate content, sulphuric acid is recommended (Horney et al., 2005), which increases soil Ca^{2+} levels by dissolving $CaCO_3$ in soils (Zia et al., 2007; Vance et al., 2008). The use of inorganic amendments are costly and labor intensive, and is an unhealthy practice for beneficial microbes.

Reclamation by Organic Amendment
The physico-chemical and biological properties of soil can be improved by the application of organic matter amendment, as they accelerate salt leaching and improve aggregate stability and water holding capacity (Walker and Bernal, 2008), thus enabling better plant growth in salt-affected soils. These are cheap and easily organic amendments which contain soil nutrients, organic matter, and enhance both cation exchange capacity and soluble exchangeable K^+, which compete with Na^+ in saline sodic soil, and limits its entry at exchangeable sites (Walker and Bernal, 2008). Examples of organic amendments include farmyard manure, poultry manure, municipal solid waste compost, and olive mill waste compost (Ahmad et al., 2006; Tejada et al., 2006; Lakhdar et al., 2009). Application of organic amendments have significant effects in an area with low rain fall but cause secondary salinization in other areas where rainfall is abundant (Diacono and Montemurro, 2011).

Biological Methods
Phyto-Reclamation
Phyto-reclamation is an environment-friendly approach to reclaim saline and saline sodic soils (Rabhi et al., 2008; Ashraf et al., 2010). In this method, salt-tolerant plant species are used to reclaim saline soil. A significant improvement in soil organic matter and water holding capacity and decrease in soluble salts and exchangeable Na^+ have been recorded (Mishra and Sharma, 2003; Nosetto et al., 2007). Salt-affected soil contains Ca in the form of calcite which is insoluble and unable to displace Na^+ from cation exchange complexes. However, the higher partial pressure of CO_2 and enhanced production of carbonic acid in the root zone could assist in the solubilization of calcite which provide soluble Ca^{2+} for exchanging Na^+ (Qadir

et al., 2005). Root exudates of salt-tolerant plant species contain H^+ which enhances Na^+ uptake and its subsequent removal from the field. Examples of halophytes include *Atriplex* spp., *Aegiceras corniculatum*, *Bruguiera gymnorrhiza*, *Chenopodium album*, *Plantago media*, *Rhizophora mucronata*, *Suaeda australis*, and *Salsola vermiculata* (Qadir et al., 2007; Hasanuzzaman et al., 2014). Phytoremediation has certain limitations in sustainable agricultural productivity, as it changes the microbial community, and takes several growing seasons to remediate polluted soil.

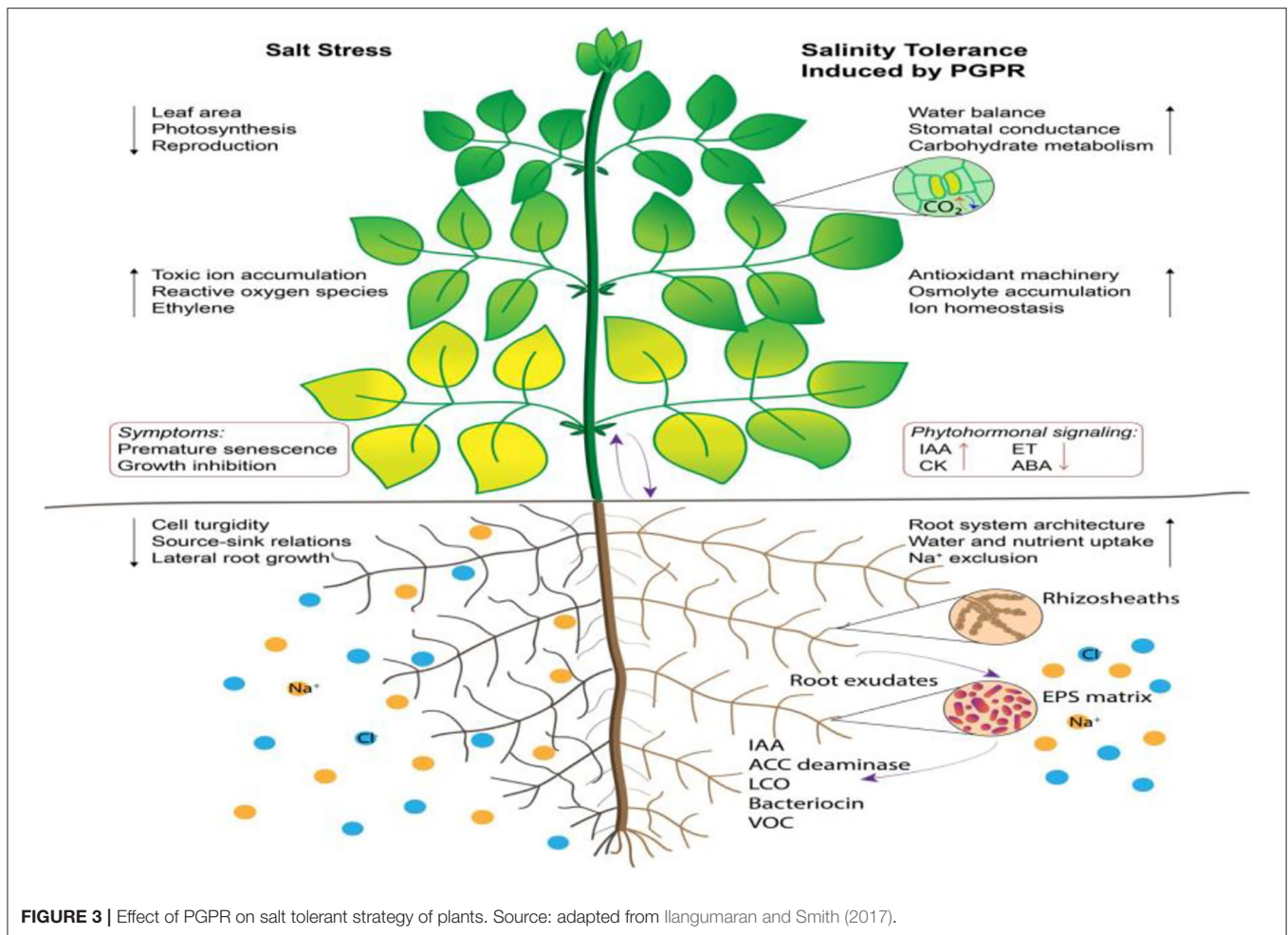## Plant Growth-Promoting Rhizobacteria for Reclamation of Saline Soils
Use of PGPR to reclaim saline soil is a far better approach than chemical and organic fertilizers because of its environment-friendly and persistent nature, with PGPR proliferating slowly and gradually in inoculated soil and ensuring their survival for decades. For this purpose, PGPR should be isolated from their native stress habitat (Sandhya et al., 2010), and reinoculated into affected fields in order to improve the soil physicochemical properties to reclaim it and in turn improve growth and yield of crops (Nosheen and Bano, 2014; Khan and Bano, 2016). A collective approach to exploit the potential of PGPR to alleviate salinity and sodicity has recently received the attention of modern agriculturalists (Arora, 2015). In the current climate change scenario, exploitation of PGPR could be an eco-friendly strategy to promote organic farming (**Figure 3**).

Salt Tolerance Mechanism of PGPR
Under saline habitats, PGPR have developed two potential mechanisms to cope against salt stress (Etesami and Beattie, 2017). The first one is "*salt in cytoplasm*" while maintaining the osmotic potential of the cell. It was discovered in halobacteria and extreme halophilic archaea (Kunte, 2009). The PGPR accumulates intracellular K^+ higher in concentration than Na^+ in the environment, as Na^+ are exported out through Na/K pumps (Sleator and Hill, 2002; Grant, 2004). The accumulation of K inside the cytoplasm helps in maintaining pH, acts as an activator of intracellular enzymes, and promotes accumulation of other compatible solutes (Epstein, 2003). The second mechanism is termed as "*organic osmolyte*" in which PGPR accumulate water soluble compatible solutes that maintain turgidity and electrolyte concentration without altering cellular metabolism and protect proteins and membranes at high salt concentration (Roberts, 2005; Tsuzauki et al., 2011; Schroeter et al., 2013; Chen et al., 2015). The osmolytes include glycerols, glutamic acid, glycine betaine, ectoine, hydroxy ectoine, proline, sugars, and trehalose (Khan et al., 2019). PGPR produces a plethora of substances which maintain the composition of outer cellular envelopes. Examples are cyclic lipopeptides (CLP) excreted by *Bacillus* and *Pseudomonas cells* (Raaijmakers et al., 2006; Banat et al., 2010).

PGPR, Climate, and Salinity
There are five main reasons why PGPR is an ideal candidate for plants: (i) their participation in C, N, P, and S cycle; (ii) immobilization of toxic ions and solubilization of essential nutrients; (iii) production of plant growth regulators; (iv) use as soil conditioner and nutrition mobilizer (Damodaran et al., 2013); and (v) induction of salinity tolerance in plants by

FIGURE 3 | Effect of PGPR on salt tolerant strategy of plants. Source: adapted from Ilangumaran and Smith (2017).

modulating higher enzymatic activities (Kannan et al., 2015). It is a cheap and eco-friendly approach which consists of living inocula of PGPR already inhabiting the soil. However, selection of the best microbe which proliferates well and improves resistance to abiotic stresses should be the first priority.
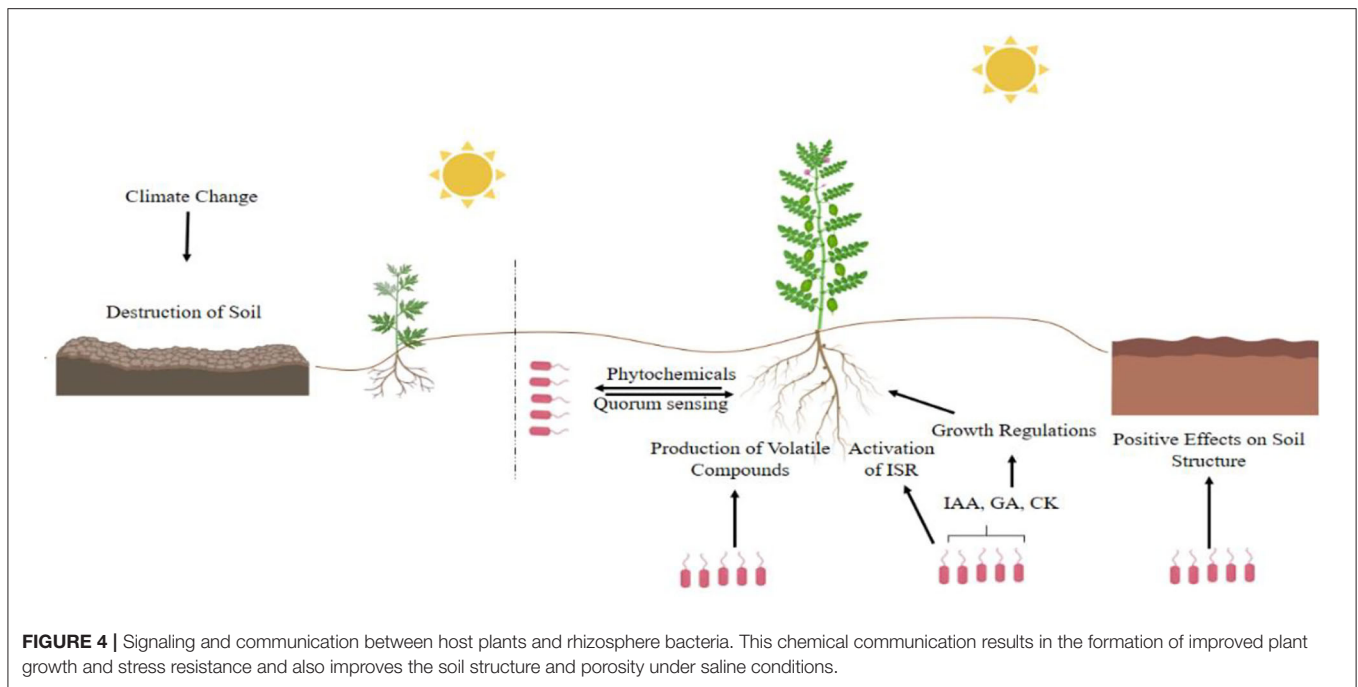
Jing et al. (2015) and Delgado-Baquerizo et al. (2016) demonstrated that change in climate (seasonal variation or temperature change) can affect diversity and effectiveness of microorganisms. Indirect effects of changes which affect the functionality and microbial community include plant biodiversity, rate, composition of root exudates of host plants, and plant composition. There are also climate-related modulations of nutrient cycling and changes in the duration of the life cycle of plants which affect microbial functioning and community too.

CHEMICAL COMMUNICATION BETWEEN PLANTS AND MICROORGANISMS

Signaling Molecules of PGPR Origin

The complex network of interkingdom signaling between plants and PGPR is governed by a number of secondary metabolites and root exudates (Bukhat et al., 2020; Khan et al., 2020a). The

nature of such communication is dynamic and influenced by a number of environmental factors. For survival and proliferation of both plants and PGPR, this cross talk is necessary because it has many advantages (the details of which are given in **Figure 4**). For interkingdom signaling the first signal that was exchanged between the host plant and its microbial partner was the flavonoid (2-phenyl-1, 4-benzopyrone derivatives) of plant origin (Rossen et al., 1985; AL-Kahtani et al., 2020). This molecule induces bacterial nod gene expression. Upon activation, *nod* gene code LCOs are secreted into bacteroids and act as a signal for the initiation of nodules. Myc-LCOs have a role in AMF symbiotic association with plants. Another interkingdom signaling system recently identified in plant-associated bacteria is based on HEHEAA molecule, which is spontaneously formed from plant-derived ethanolamine. It acts as a signal for LuxR solo, PipR, which is the co-inducer of *pipA* in plant root endophytic bacterium *Pseudomonas* GM79 (Coutinho et al., 2018). Bacteria produce extracellular chemical signals, which control different phenotypes in bacteria and also help in establishing an association with plants. The idea of quorum sensing (QS) signal molecules came from the discovery of autoinduction in marine bacteria *Vibrio fischeri*. In this phenomenon, bacteria produce an autoinducer signal called

FIGURE 4 | Signaling and communication between host plants and rhizosphere bacteria. This chemical communication results in the formation of improved plant growth and stress resistance and also improves the soil structure and porosity under saline conditions.

homoserine lactones (AHLs) which induces bioluminescence when population density reaches a specific threshold level. So, this phenomenon was named autoinduction. Primary signal molecules generated by bacteria in QS are autoinducers which are either AHLs, quinoline signals, autoinducer-2 (AI-2), auto inducing peptides (AIPs), cyclic dipeptide, indole, short peptides, diffusible signal factors (DSF), or pheromones. AHLs were the first autoinducers identified in gram negative bacteria that regulate the QS phenomenon through LuxI/LuR regulatory proteins. In gram positive bacteria this process is regulated by small peptide autoinducers.
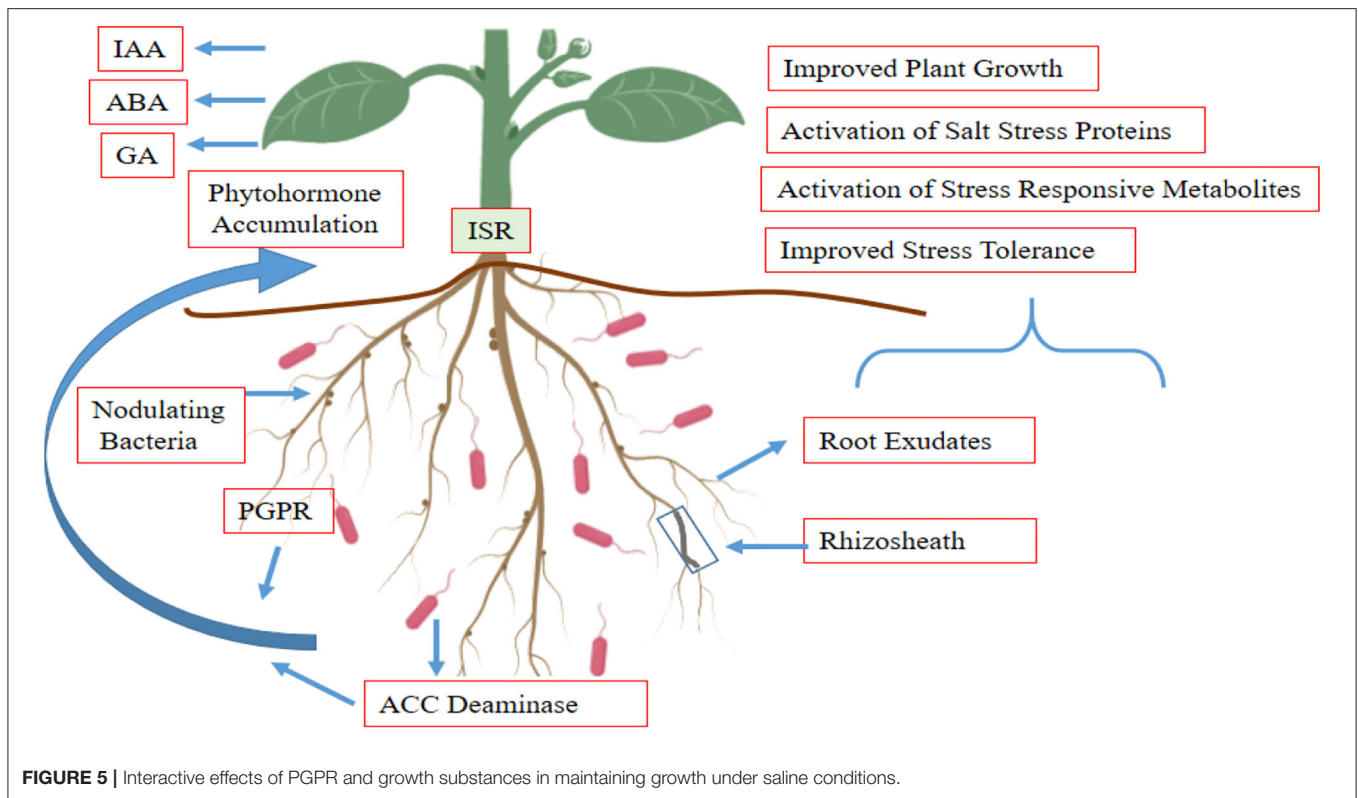
Antibiotics are another potential class of bacterial signaling molecule. Ethanolamine acetamide is an active inducer for the PipR transcription regulator in root endophyte *Pseudomonas* sp. GM79 (Coutinho et al., 2018). It is also present in leaf macerates of *Populus*. Microbes secrete phytohormone that act as growth and defense regulators to plants, i.e., gibberellic acid (GA), cytokinin (CK), abscisic acid (ABA), indole acetic acid (IAA), and jasmonic acid (JA). Volatile compounds (VOCs) are another class of molecules present in extracellular products of microbes that modulate plant growth and maintain soil health (**Figure 5**). These include terpenes, nitrogen compounds, pyrazines, indole, and volatile sulfur compounds (Pandey et al., 2013; Groenhagen et al., 2014; Song et al., 2015; Tyc et al., 2015). EPS secreting PGPR helps in stabilizing soil physicochemical properties, improving water holding capacity and CEC (Upadhyay et al., 2012). Some secondary metabolites act as signaling molecules, i.e., in response to flavonoids present in root exudates, and PGPR secrete nod factor which initiates nodule formation in host plants (Miransari and Smith, 2009). A thuricin compound extracted from B. thuringiensis enhances tolerance of *Arabidopsis thaliana* against

250 mM NaCl (Subramanian, 2013). Polyamine secreting PGPR if inoculated to plants and promotes root architecture and stomatal conductance against stress conditions (Zhou et al., 2016). The above-mentioned examples of signaling molecules along with thousands of others mediate a complex network of signaling in rhizosphere which may be (i) quorum sensing-based microbial intra or inter species signaling, (ii) plant to microbe via plant based signals, or (iii) signaling from microbes to plants.

Signaling Molecules of Plants Origin

Many compounds of root exudates act as general chemoattractant i.e., arabinogalactan protein exuded from plant root tips into the rhizosphere to attract beneficial microbes and repel pathogens. Sugars and organic acids present in the root exudates serve as growth factors and mediate antifungal activities in certain microbes (Khan et al., 2018a). Citric acid and fumaric acid present in root exudates attract microbes and help in biofilm formation (Neal et al., 2012; Zhang et al., 2014). Flavonoids present in root exudates act as an important signal for nodule formation by inducing bacterial *nod* genes.

Strigolactones (SLs) and cutin monomers are plant-derived signals perceived by both beneficial and pathogenic bacteria (Smith, 2014). SLs belong to plant terpenoid lactones and are involved in plant fungus symbiosis. In Pi-deficient soil, SLs induce the inhibition of shoot branching in host plants and stimulate the growth of arbuscular mycorrhiza fungi (AMF) by increasing hyphal branching toward the host. During AMF infection, Myc factor is also secreted by AMF which stimulates common symbiosis signaling pathway (CSSP) or Sym (Shahid et al., 2020). Myc factors induce lateral root development by increasing root area and by providing starch to fungi to

FIGURE 5 | Interactive effects of PGPR and growth substances in maintaining growth under saline conditions.

establish symbiosis. As the CSSP pathway triggers, intracellular Ca^{2+} spiking occurs, which activates CCaMK, which in turn activates transcription of certain genes responsible for symbiosis establishment. The next step is the formation of a pre-symbiotic structure known as hyphopodium by mature hyphae. It facilitates the penetration of AMF into the roots. RAM2 gene is responsible for the formation of hyphopodium. This gene encodes glycerol-3-phosphate acyl transferase enzyme which degrades cutin monomers in the plant cell wall. Thus, cutin monomers act as a plant signal for the formation of hyphopodium. At het same time, host root cells form PPA (Pre-penetration apparatus) which direct the path for AMF colonization from hyphopodium to intracellular space, and a new structure is formed called arbuscule. The entering of AMF hyphae into the root cortex and formation of arbuscule is controlled by the Sym pathway.

Another important molecule present in root exudate is lysophosphatidylcholine which regulates the phosphate transporter gene in fungi and ensures the monitoring of Pi available to plants. In the case of ectomycorrhizal fungi (EMF), the signaling molecules that control the association with host plants are of different classes i.e., abietic acid, flavonoid rutin, hesperidin, quercetin, and chrysin compounds in root exudates lead to germination of EMF. These fungi also secrete phytohormones which should influence root morphology before the establishment of a symbiotic structure, as they reduce the growth of lateral roots where EMF establish. EMF also secrete a signaling molecule hypaphorine, an amino acid derivative which induces these morphological changes. Phenolic acids

synthesized by plants are involved in plant-microbe symbiotic association, and AMF symbiosis also plays a role in plant defense. Phytoalexins are secreted by wounded plants to repel or kill microbes. Flavonoids act as chemoattractant to rhizobia and induce the expression of nod gene by synthesis of LCOs. Coumarins are phenolic compounds found across a wide variety of plant species and have a role in iron acquisition and modulating root microbiome composition. Using synthetic community (SynCom) inoculation, it was found that the abundance of *Pseudomonas* was higher in coumarin deficient *Arabidopsis* as compared to wild type, because wild type generated a specific coumarin, sideretin, which had a toxic effect by generating H_2O_2 so it caused toxicity to *Pseudomonas* strain (Khan et al., 2019; Voges et al., 2019).

Benzoxazinoids belong to indole-derived metabolites in plants that control belowground and above ground interactions. Correlating LC-MS metabolite profiling with operation taxonomic unit (OUT) sequencing data showed that benzoxazinoid stimulates the abundance of Methylophilaceae bacteria while repressing the abundance of Xanthomonadaceae bacteria. Camalexin is another indole compound which can modulate the functionality of root associated microbes (Khan et al., 2020b). Plant microbe interaction assay showed that this compound plays a key role in modulating the effectiveness of growth promoting bacteria because camalexin deficient *Arabidopsis* mutants were unable to receive growth promoting potentials that were provided by mutualistic strains. As root exudate shape microbe community, at the same time microbes

also influence the root exudate composition. For example, microbe's metabolite 2,4-DAPG and zearalenone alter the amino acid composition of tomato in order to maintain osmoregulation (Weller et al., 2007).

Secondary Metabolites Nature on the Basis of Function

A diverse group of bioactive metabolites are produced by PGPR which are not important for normal growth and development but play an important role in stress conditions. On the basis of function, they are categorized into growth hormones, chelating compounds, antibiotics, antifungal, antitumor, and pigment compounds (Guo et al., 2013; Olanrewaju et al., 2017; Asadullah et al., 2020). Examples of such bioactive metabolites include 2, 4-diacetylphloroglucinol (DAPG), amphisin, HCN, phenazine, pyoluteorin, tensin, oligomycin A, xanthobaccin, and zwittermicin. One important role of siderophore secreting PGPR is their ability to reduce Fe availability to phytopathogens and render their proliferation (Olanrewaju et al., 2017). *P. putida* secretes Putidacin siderophore which is effective against phytopathogens (Parret et al., 2003). Some metabolites are soluble in nature, i.e., ribosomal peptides, non-ribosomal peptides, and polyketides. Pyoverdine is an example of a non-ribosomal peptide, which acts as an iron chelating compound (Hider and Kong, 2010; Khan et al., 2018b).

Positive Impacts of Chemical Communication on Agricultural Productivity

Literature has reported on the potential role of PGPR in marinating the growth and yields of crops under different stress conditions (**Table 1**). GC-MS analysis showed that *Cronobacter*

sp. JZ38 produce indole and sulfur VOCs which possess volatile mediated antagonistic activity against *Phytophthora infestans* in plate assay and also act as growth inducer by promoting root and shoot biomass in *Arabidopsis thaliana* under contact assay (Eida et al., 2020). Due to the difference in AHLs structure, plant response also varies. AHL with short acyl chains increase root growth and primary root elongation in *Arabidopsis thaliana*, while AHL with long acyl chains induce resistance. This phenomenon is known as AHL priming. Rodríguez et al. (2020) evaluated the antagonistic behavior of *Pseudomonas segetis* P6 (isolated from *Salicornia europaea* rhizosphere) against phytopathogens. This bacterium produced an enzyme penicillin acylase which had degraded AHLs extracted from crude extract of bacterial phytopathogens. The strain P6 inhibited the virulence caused by pathogens through secretions of AHLs. When plants were observed, no symptoms of soft rot were found in potato tuber and carrot slice assay. An experiment was conducted on *Trichoderma asperellum* and *B. amyloliquefaciens* following simultaneous and sequential inoculation method (Karuppiah et al., 2019). The expression of defense-related vital genes and secondary metabolites were upregulated in *Trichoderma* and down regulated in *Bacillus*. Thiamine, an important cofactor for the biosynthesis of IAA in plants, was upregulated in *Trichoderma* and increased root length in maize plants' under biotic stress condition. Pipecolic acid was detected under a simultaneous inoculation of plants with beneficial microbes that induced systemic acquired resistance (SAR). Aminoglycoside is a low molecular weight antibiotic and pyocyanin is a pigment producing molecule secreted by *P. aeruginosa*; both act as signaling molecules and induce the development of biofilm by *rhizobia* species. Cis-2-dodecenoic acid is a type of diffusive

TABLE 1 | Alleviation of different stresses in crops by PGPR.

PGPR	Crop	Stress	Mechanism	References
B. amyloliquefaciens	Rice	Salinity	Increase the plant height, leaf size, root length and dry matter.	Nautiyal et al., 2013
B. cereus, P. moraviensis	*Triticum aestivum*	Saline sodic	Alleviate the effect Cu, Cr, Co, Cd, Ni, Mn, Pb and improve growth.	Hassan et al., 2017
B. subtilis BMB26	*Cucumis melo*	Disease	Control sclerotium rot disease caused by *Sclerotium rolfsii*.	Darma et al., 2016
B. subtilis, B. atrophaeus, B. sphaericus	Strawberry	Salinity	Increase biomass of strawberry.	Karlidag et al., 2013
B. subtilis and Arthobacter sp	Wheat	Salinity	Impact on growth oxidative status.	Upadhyay et al., 2012
P. fluorescens, Variovorax sp.	*Brassica napus*	Heavy metal	Improve the phytoextraction of Cd, Cu, Pb, Zn by *Brassica napus*.	Dabrowska et al., 2017
Burkholderia cepacia MPC-7	Pepper	Disease	Secrete organic acids that stop the growth of *Phytophthora capsici*.	Sopheareth et al., 2013
Microbacterium, Curtobacterium	Brassica nigra	Heavy metal	Alleviate the adverse effect of Zn, Pb, Cu, As. Improve germination.	Roman-Ponce et al., 2017
P. putida, B. pumilus, L. sphaericus, Ex. aurantiacum	Maize	Saline sodic and heavy metals stress	Improved soil physico-chemical properties reduced the uptaKe of Ni, Cr and Pb, enhanced yield.	Ullah and Bano, 2019
P. fluorescens strain ALEB 7B	*Atractylodes lancea*	Pest pathogen attack	Secrete 2-Piperidonone, inhibits the growth of phytopathogenic *A. rolfsii*.	Zhou et al., 2014
Stenotrophomonas maltophilia SBP-9	Wheat	Salinity	Defense response against *Fusarium graminearum* and improve growth.	Singh and Jha, 2017

signal factor (DSF) secreted by *Burkholderia cenocepacia*. It inhibits the growth of fungal pathogens such as *Candida albicans*. Luteolin is a strigolactone present in root exudates of *Medicago truncatula* and acts as a chemoattractant for *rhizobia* to induce nod gene expression. Wild type DIMBOA maize produces more benzoxazinoid and attracts more *P. putida* than DIMBOA deficient mutant maize. It was demonstrated in a study that the spraying of leaf spot pathogen of tomato (*P. syringae*) on *Arabidopsis thaliana* resulted in a higher proportion of malic acid in root exudates. The presence of aromatic acid in root exudates recruited a large number of plant growth-promoting *B. subtilis*. Root exudates of *Ocimum basilicum* contain rosmarinic acid which showed antagonistic activity against pathogenic *Pythium*. Hao et al. (2016) reported that volatiles released from *B. amyloliquefaciens* FZB42 promoted biomass of *Arabidopsis thaliana*, and a study conducted by Asari et al. (2016) revealed that seedlings of *Arabidopsis thaliana* exhibited a 2-fold increase in fresh and dry weight after 18 days of exposition to volatiles emitted from *B. amyloliquefaciens*.

PGPR secrete and modulate the concentration of auxin (IAA), cytokinin, gibberellins (GA), ethylene, and abscisic acids (ABA) in plants which regulate various metabolic activities (Egamberdieva and Kucharova, 2009; Waadt et al., 2015; Wani et al., 2016; Khan et al., 2018a). IAA, a physiologically active hormone produced by almost 80% soil microflora, utilizes tryptophan as precursor molecule (Li et al., 2018; Khan et al., 2020a). This hormone is primarily involved in cell division, morphogenesis, elongation of plants, and ultimately improved growth of shoots and yield (Asim et al., 2013; Ahemad and Kibret, 2014; Bhardwaj et al., 2014). *Pseudomonas* sp. are well-known IAA producers (Reetha et al., 2014; Kumar et al., 2015; Khan et al., 2020b), along with the secretion of organic acids like gluconic acid which solubilize insoluble phosphate and ease their availability to plants (Otieno et al., 2015; Mishra et al., 2018; Sarkar et al., 2018). Spaepen et al. (2008) reported morpho-physiological changes in root architecture upon inoculation with *Azospirillum* strain which was tested *in vitro* for phytohormone (IAA, GA, and Cytokinin) production potential. A similar outcome on wheat root morphology was demonstrated by Sadeghi et al. (2012) after being treated with *Streptomyces*. Another study to strengthen PGPR's role in plant growth promotion by signaling and regulating phytohormone level was presented by Arkhipova et al. (2007), who found remarkable signaling of cytokinin from root to shoot after root inoculation with cytokinin synthesizing bacteria *B. subtilis*.

GA facilitates germination and elongation of stem, flower, and fruit setting (Cassán et al., 2001; Hayat et al., 2010; Pandya and Desai, 2014). PGPR also secrete abscisic acid, which stimulates growth activities under stress. It is secreted by many PGPR such as *Azospirillum brasilense, Bacillus subtilis, Bacillus licheniformis,* and *Pseudomonas putida* (Cohen et al., 2008; Dos Santos et al., 2020; Kousar et al., 2020). Ethylene is a gaseous hormone which controls fruit ripening (Masood et al., 2012; Nazar et al., 2014). However, under salt stress elevated levels of ethylene arrest different physiological activities of plants. PGPR modulate ethylene level by hydrolyzing ACC into NH_3 and α-ketobutyrate (Siddikee et al., 2010; Gamalero and Glick, 2015; Ali and Kim,

2018) and reduce the deleterious effect of ethylene under salinity stress (Bal et al., 2013; Han et al., 2015). Under salinity stress, rice growth is significantly increased when treated with ABA producing PGPR over control (Shahzad et al., 2017; Billah et al., 2020). It was confirmed by Zhou et al. (2017) when he inoculated *Chrysanthemum* with ABA producing *B. licheniformis* under saline condition; a significant increase in seedling establishment, biomass, and photosynthesis was recorded over control plants.

One of the most important mechanisms to combat salinity stress is the production of compatible solutes. These are low molecular weight compounds that have a key role in mitigating the adverse effect of salt stress. Proline is the most studied osmolyte under salt stress, which has been reported in plants inoculated with PGPR. It has a synergetic effect on the production of other computable solutes under induced salt stress. For example, proline is involved in the synthesis of trehalose, another osmolyte in plants when inoculated with PGPR (Chen et al., 2007). Similarly, an increased concentration of total soluble sugar modulated by leaf protein content has been recorded in plants treated with PGPR (Upadhyay and Singh, 2015). Another class of osmoprotectant is glycine betaine which maintains higher leaf water potential during stress conditions (Hoque et al., 2007; Peng et al., 2008). Inoculation of maize with rhizobacteria significantly improved proline, total soluble sugar, and phenolic contents under salt-affected field condition (Iqbal et al., 2016). *De novo* synthesis of proline in *Azospirillum* can boost the wheat plant's endogenous proline accumulation (Han and Lee, 2005). Paul et al. (2005) found that *P. pseudoalcaligenes* combat high salt concentration via the production of Ala, Gly, Glu, Ser, Thr, and Asp amino acids, which help in osmotic adjustments as well as in the correct folding of polypeptide chains for maintaining structurally stable proteins under adverse environmental conditions (Streets et al., 2006). The strategy adapted for stress alleviation by these microbes includes modification of chemical constituents through deposition or alteration in capsular compounds to enhance water retention and carbon diffusion by providing micro-environment as reported in *P. fluorescens* (Ali et al., 2009). Moreover, salt-responsive genes' expression in a halophilic PGPR, such as *P. pseudoalcaligenes* and *B. subtilis*, encode a wide range of stress proteins which behave as chaperones for cellular macromolecules (Volker et al., 1994; Paul et al., 2005).

Climate change has adversely affected soil nutrient and fertility status (Pareek, 2017). This problem can be overcome by the application of PGPR which improve soil nutrient status and their uptake into plants through the release of nitrogenase, phosphatase, dehydrogenase, siderophores, and exopolysaccharides (Arshad et al., 2008; Cohen et al., 2009). Decline in CO_2 fixation due to hyper osmosis cause the production of reactive oxygen species (ROS), which alter the physiology and histology of plants through changes in normal metabolic activities, damage to the phospholipid bilayer, and ultimately cell apoptosis (Johnson et al., 2003; Hichem et al., 2009; Miller et al., 2010; Halo et al., 2015). PGPR activates antioxidants and defense-related enzymes in plants and help in the mitigation of ROS (Chakraborty et al., 2013). To protect plants against oxidative stress and mimic the harmful effect

of H_2O_2, plants have been inoculated with PGPR (Kim et al., 2005; Upadhyay et al., 2012). The inoculation has significantly enhanced the antioxidant enzymatic system and mitigated the adverse effect of salt stress as compared to control (Damodaran et al., 2013; Jha and Subramanian, 2013). *B. megaterium* and *Enterobacter* sp. modulate ROS scavenging enzyme (SOD, CAT, APX) in *Abelmoschus esculentus* when grown under saline condition (Habib et al., 2016; Khan et al., 2018b).

CONCLUSION AND FUTURE PERSPECTIVES

Climate change has negatively impacted the duration and intensity of seasonal changes e.g., a reduced winter season with less snow fall followed by abrupt run off in early spring, subsequently resulting in flood inundation in different areas of the world. The increased temperature during daytime in summer resulted in high evapo-transpiration that resulted in the accumulation of salt on the soil surface. It has adversely impacted physicochemical properties of agricultural land. PGPR had stimulatory effects on the growth and physiology of the plant under induced salt stress. They increased the availability of essential nutrients K and Ca, enhanced Fe and Zn in the rhizosphere soil, and enhanced the uptake by roots and its translocation to leaves and grain. The PGPR induced

salt tolerances is mediated by the production of secondary metabolites which have antimicrobial and anti-larvicidal and act as signaling molecules. It is mediated by the presence of ACC deaminase and IAA production. PGPR induces tolerance against salinity by enhancing root proliferation and root biomass and improving the water use efficiency of wheat. This minimizes the oxidative stresses but improves osmoregulation. PGPR, the natural microflora, have adopted different strategies to cope with the changing climate. Under salt stress they produce different kinds of bioactive metabolites which help in their persistence as well as providing a synergetic effect to plant growth and yield. Therefore, ideal candidates of PGPR should be selected for better agriculture productivity in salt-affected areas.

AUTHOR CONTRIBUTIONS

AU: formal analysis, investigation, methodology, software, validation, visualization, writing-original draft, writing-review, and editing. AB: conceptualization, data curation, formal analysis, investigation, project administration, resources, supervision, writing-original draft, writing-review, and editing. NK: conceptualization, data curation, formal analysis, project administration, resources, software, supervision, validation, writing-original draft, writing-review, and editing. All authors contributed to the article and approved the submitted version.

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