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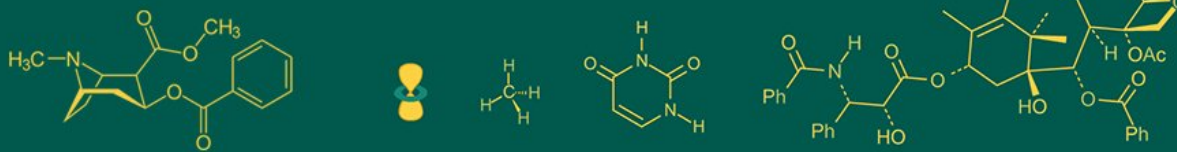
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Soil microbiome: Applications and mechanisms for salinity stress mitigation in plant and soil ecology: A review

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Abstract
Soil health is paramount for sustainable agriculture, impacting crop production, nutrient cycling, and ecosystem stability. The microbial communities inhabiting diverse environments, termed microbiomes, play crucial roles in soil health and ecosystem functions. Among various stresses affecting plant growth, salinity stress poses significant challenges, resulting from high concentrations of soluble salts in the soil. This stress disrupts physiological processes in plants, impeding growth and productivity. Globally, extensive areas of agricultural lands face salinity issues, leading to substantial economic losses. Physiological responses of plants to salinity stress include osmotic and ionic stresses, as well as oxidative stress. Halophytes, adapted to high salt concentrations, contrast with glycophytes, which are more susceptible to salinity stress. The impact of salinity stress on plants extends from osmotic stress to ionic toxicity, affecting nutrient uptake, photosynthesis, and reproductive development. This review paper focuses on microorganisms, particularly salt tolerant plant growth promoting rhizobacteria (ST-PGPRs), which employ various strategies to mitigate salinity stress in plants. These strategies encompass cellular adjustments, salt-in approaches, osmolyte accumulation, and direct and indirect mechanisms for plant growth promotion. Direct mechanisms include nitrogen fixation, phosphorous solubilization, ammonia production, and the production of plant hormones. Indirect mechanisms involve the synthesis of ACC deaminase, Trehalose, siderophores, antioxidant enzymes, Hydrogen cyanide, Exopolysaccharide, Nitric oxide, ion homeostasis and compartmentalization, and biofilm formation. Understanding these microbial strategies is crucial for developing sustainable agricultural practices in saline soils, ultimately enhancing soil health and agricultural productivity in salt-affected regions.

Keywords: Abiotic stress, anti-oxidant, salinity, halophiles, halotolerant, ACC deaminase, exopolysaccharide, glycophytes, HCN, ion homeostasis, ionic stress, microbiomes, osmolytes, osmotic stress, oxidative stress, ROS and ST-PGPR

Introduction
Soil health is crucial for sustainable agriculture, affecting crop production, nutrient circulation, and ecosystem stability (FAO, 2015) [42]. Recognizing soil as a finite, non-renewable resource within human timescales is essential. Moreover, soil holds cultural importance, supporting terrestrial life fundamentally (Gaikwad et al., 2023) [45]. A unique microbial community inhabits distinct environments with specific physio-chemical properties, collectively known as microbiomes. Microbiomes encompass microorganisms, their genetic material, proteins, lipids, polysaccharides, and metabolites, reflecting a comprehensive view. This concept extends to the microorganism's activities, such as their spatial and temporal dynamics, shaping specific ecological niches. In plants, the microbiome represents a cooperative assembly of microorganisms within and around plants, forming a cohesive ecosystem. Similarly, the soil microbiome comprises diverse microorganisms crucial for ecosystem functions like nutrient cycling, soil structure maintenance, and pathogen control. The plant-soil microbiome denotes the dynamic community of bacteria, archaea, and fungi interacting with plants and soil, influencing plant growth and agricultural productivity. Stress within a plant encompasses external factors that detrimentally influence its growth, development, and productivity (Gull et al., 2019) [53]. These stresses are broadly classified into biotic and abiotic categories.

Biotic stress arises from living organisms such as animals, pathogenic nematodes, insects, weeds, and microbes, while abiotic stress stems from physical factors like temperature fluctuations, salinity, drought, waterlogging, and heavy metal toxicity (Kumar *et al*., 2020) [73]. These biotic and abiotic stresses represent unfavourable ecological conditions that impede crop plants from reaching their full genetic potential, leading to significant yield losses (Figure 1) (Goswami and Deka, 2020) [51].
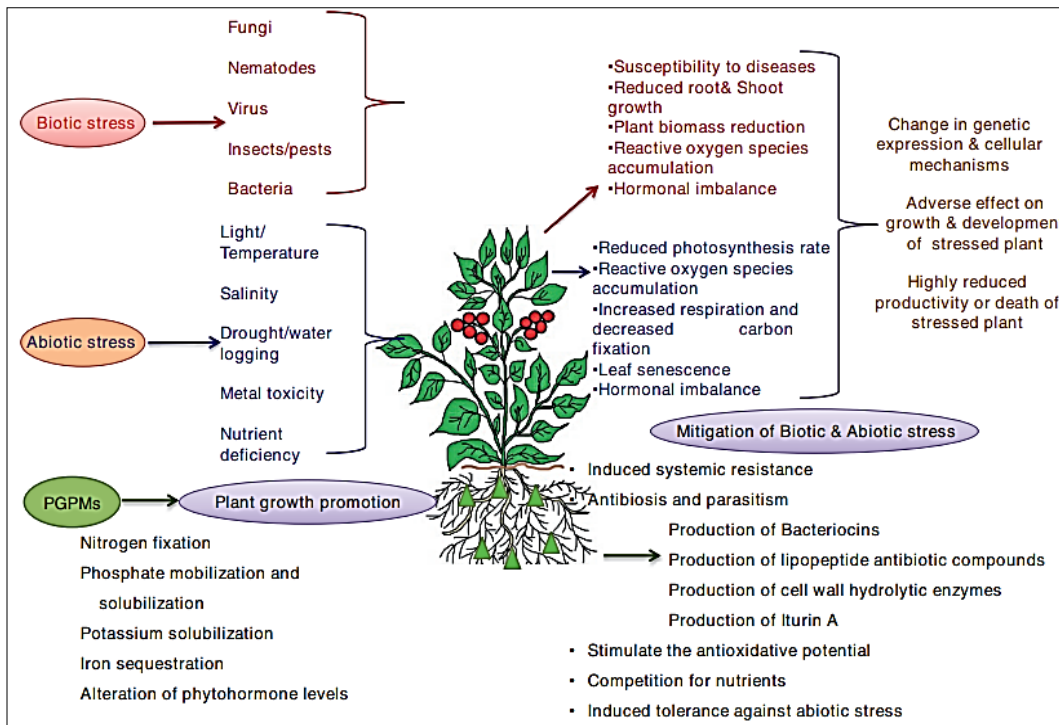

Fig 1: Impacts of diverse stress on plant physiology (adapted from Hussain *et al*., 2022)

Plants due to their stationary nature, encounter various fluctuations in their surroundings. Unlike animals, which can mitigate these variations through adaptations and mobility, plants rely on internal metabolic processes to adjust to changing environmental conditions. A plant's response to stress typically manifests as either elastic, where the plant temporarily returns to its original state, or plastic, where there are irreversible changes in physiology or morphology. These responses to stress are intricate and involve various physiological adjustments (Figure 2).
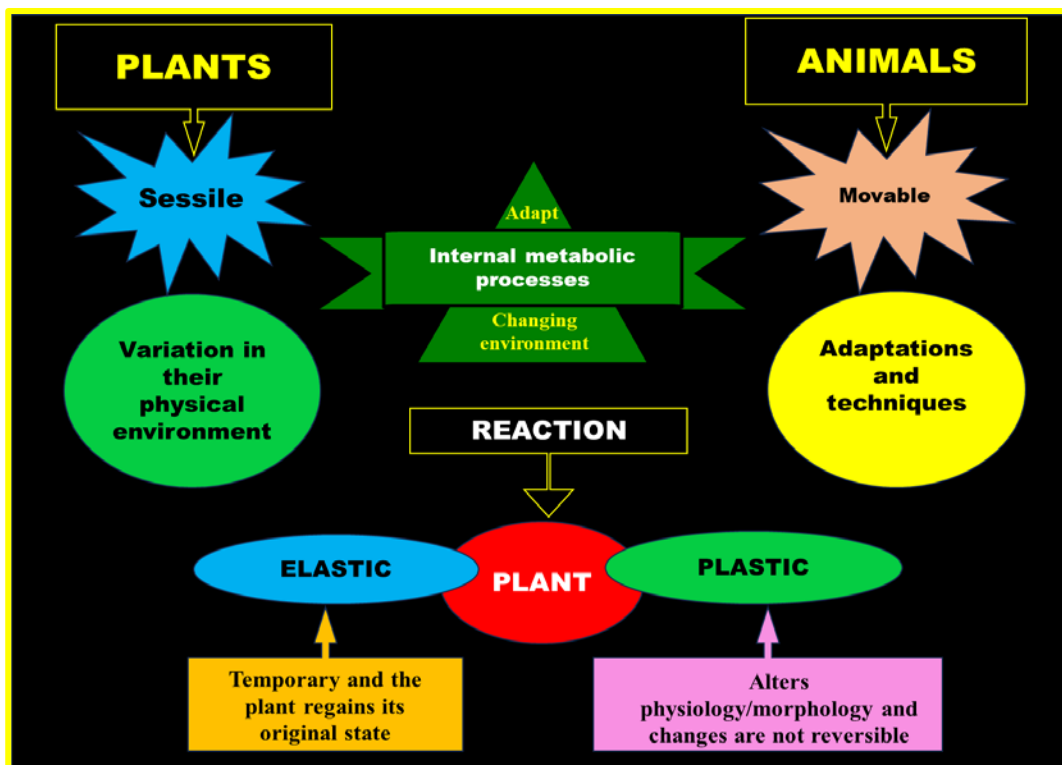

Fig 2: Adaptive responses of plants to environmental stress

Plant microbiome: Plant growth-promoting microbes and abiotic stresses

The captivating variety of microorganisms, including both harmful and beneficial fungi, bacteria, oomycetes, and archaea, found within plant roots and in the surrounding soil known as the rhizosphere collectively form the microbiome. These beneficial soil microbes in the rhizosphere play a crucial role in aiding nutrient absorption and promoting plant growth (Pascale *et al*., 2020) [108].

Plants, being stationary, constantly adjust their metabolism to counter various stresses (Gull *et al*., 2019) [53], striving to adapt to changing environmental conditions, a process termed acclimatization (Singh *et al*., 2018) [139-140]. Despite these efforts, many plants, particularly crops, struggle to fully acclimatize to abiotic conditions. Prolonged exposure to such stresses adversely affects plant physiology, leading to stunted growth, improper development, or even death. Plant breeders have employed various biotechnological methods to develop stress-tolerant plants, but this is a challenging and time-consuming endeavour. In such circumstances, plant growth promoting microorganisms (PGPMs) present in the soil can play a crucial role (Kumar and Verma, 2018) [72]. Abiotic stresses trigger the expression of stress-tolerant genes involved in protecting cell membranes and proteins through signaling and transcriptional control. Overexpression of these genes enables plants to withstand specific stress conditions (Saravanakumar *et al*., 2011) [128]. Certain PGPMs, particularly plant growth-promoting rhizobacteria (PGPR), plant growth-promoting fungi (PGPF), and endophytes, bring about physiological and biochemical alterations in stressed plants by amplifying the expression of stress-tolerant genes. These encompass genes associated with abscisic acid (ABA) signaling, known to improve drought resistance and grain yield under water stress conditions, as well as auxin signaling genes linked to lowering reactive oxygen levels in plants. Additionally, gibberellic acid (GA) signaling, which activates certain transcription factors, contributes to this process, termed induced systemic tolerance (IST). PGPR genera like *Azotobacter*, *Klebsiella*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Variovorax*, *Serratia*, *Burkholderia*, *Pseudomonas*, along with arbuscular mycorrhizal (AM) fungi and endophytic fungi such as *Trichoderma* spp., not only promote plant growth under optimal circumstances but also under both biotic and abiotic stressors. The contributions of these beneficial microorganisms in alleviating major stresses in plants are discussed individually (Table 1).

Table 1: Stress responsive plant growth promoting rhizobacteria

Abiotic stress			Biotic stress
Salinity	Drought	Temperature	
Azospirillum brasilense	*Achromobacter pechaudii*	*Burkholderia phytofirman*	*Paenibacillus polymyxa* (strains b2,3,4)
Pseudomonas syringae	*Acinetobacter* sp.	*Pseudomonas* sp. *(strain akm-p)*	*Paenibacillus favisporus* (strain bkb30)
Pseudomonas fluorescens	*Pseudomonas fluorescens*	*Pseudomonas putida (strain akm-p7)*	*Bacillus amyloliquefaciens* (strain hyd-b17)
	Pseudomonas sp.	*Aeromonas hydrophila*	*Bacillus licheniformis* (strain hytapb18),
	Bacillus subtilis	*Serratia liquefaciens*	

Plant growth-promoting rhizobacteria (PGPR)

Biotic stress from agents like viruses, bacteria, nematodes, weeds, and arachnids can disrupt plant growth and metabolism. Some of these bio-agents can cause plant mortality, while others form symbiotic relationships with plants. Certain beneficial microbes, like plant growth-promoting rhizobacteria (PGPR) (Figure 3), aid plant growth by colonizing roots and stimulating root and shoot growth (Hashem *et al*., 2019) [60]. PGPR also enhance nutrient uptake through mechanisms like nitrogen fixation. Various bacteria found in the plant rhizosphere, including species like *Bacillus*, *Azospirillum* and *Pseudomonas*, promote plant growth. Globally, biological nitrogen fixation, primarily through symbiotic associations with species like *Rhizobium* and *Frankia*, contributes significantly to nitrogen availability for plants, thereby mitigating biotic and abiotic stresses (Saharan and Nehra, 2011) [125].
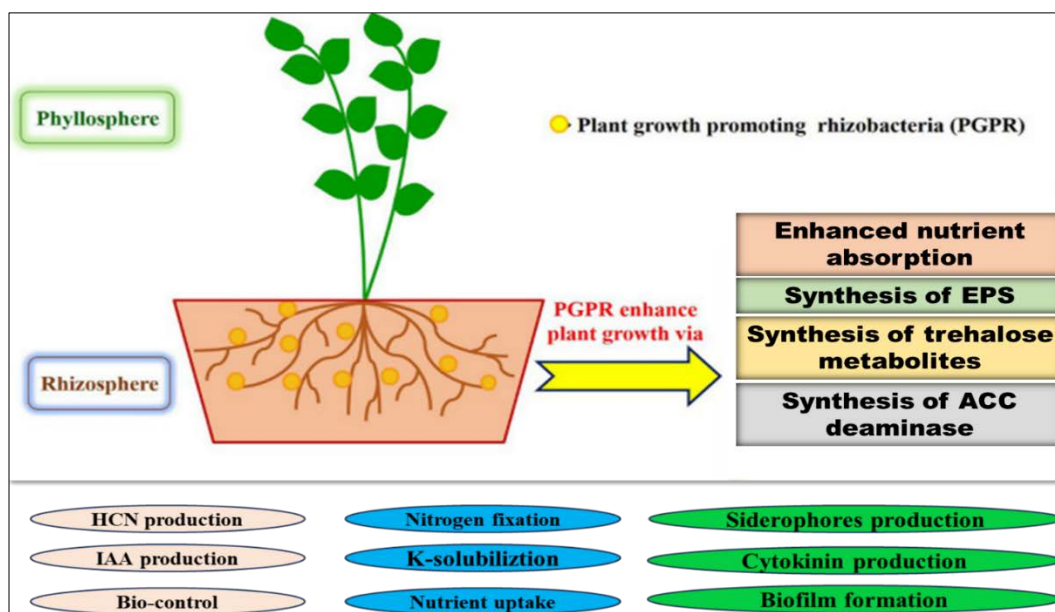

Fig 3: Role of plant growth-promoting rhizobacteria (adapted from Jha *et al*., 2022)

Plant growth-promoting fungi (PGPF)

The diverse genera of non-pathogenic fungi, known as plant growth-promoting fungi (PGPF), colonize roots, enhancing plant growth and aiding in disease suppression and induced systemic resistance (Figure 4). PGPF play a crucial role in sustainable agriculture, promoting crop production in an environmentally friendly manner (Mandal, 2019) [87]. They directly enhance various aspects of plant growth and development and indirectly regulate it by suppressing pathogens and mitigating stress (Hossain and Sultana, 2020) [62]. PGPF, like *Trichoderma* spp., help plants adapt to stress conditions (Guler *et al*., 2016) [52]. They also protect plants from heavy metal stress in polluted environments (Li *et al*., 2012) [78].
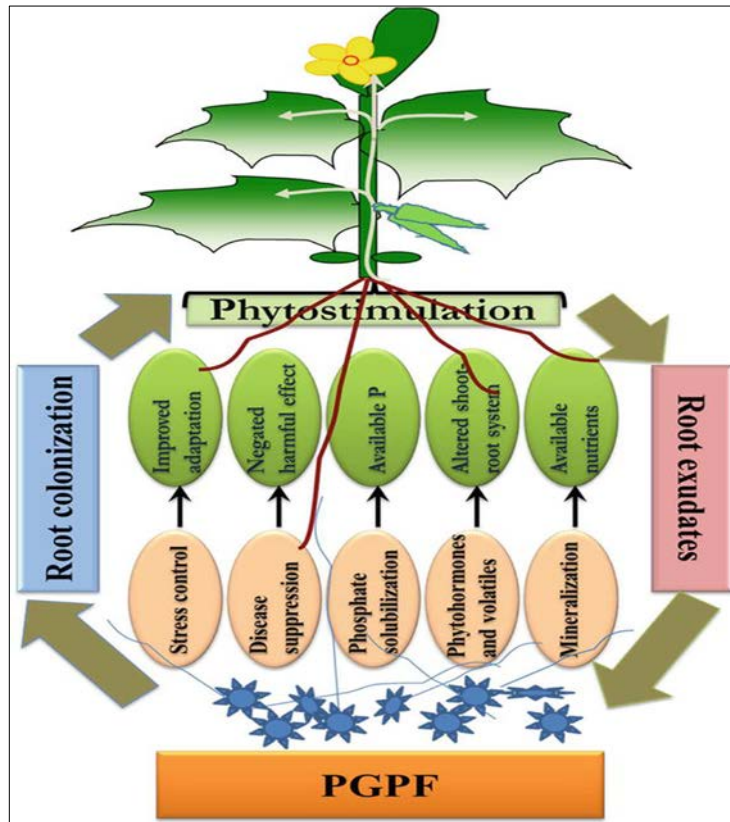

Fig 4: Role of plant growth-promoting fungi (PGPF) (adapted from Hossain and Sultana, 2020) [62]

Salinity stress

Soil salinization stands as a critical impediment, significantly impacting global food production. The factors accountable for salinization contribute to the deterioration of soil's physical, chemical, and biological attributes. Soil salinity denotes the concentration of soluble salts in the soil, typically measured through electrical conductivity (EC) (Chesworth, 2007) [28], expressed in deci-Siemens (dS) per meter at 25 °C (1dS/m = 1mmho/cm). Sodium chloride emerges as the predominant water-soluble salt in salt-affected soils, breaking down into sodium (Na^+) and chloride (Cl^-) ions upon dissolution (Figure 5). These ions induce both osmotic and ionic stress in higher plants, especially in glycophyte species (Cha-um and Kirdmanee, 2011) [24]. Salt-affected soils are classified into saline, saline-sodic and sodic soils (Table 2).
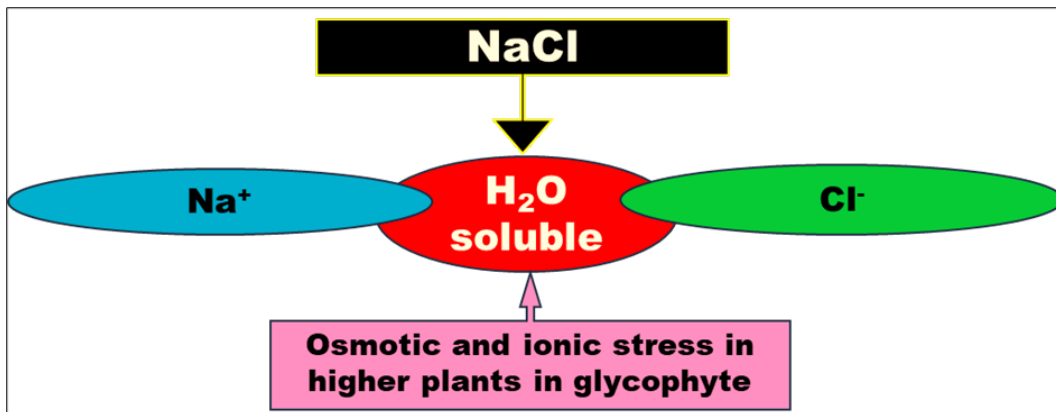

Fig 5: Ion dissociation of sodium chloride in aqueous solution

Table 2: Classification of salt affected soils

Soil type	Salt present	pH	Ece dSm^{-1}	SAR	ESP	Structure Condition	Salt Conc.
Saline soil	*N* soluble salts Ca, Mg, K, Na	< 8.5	> 4	< 13	< 15	Flocculated	> 0.1%
Saline-sodic soil	Both salts	< 8.5	> 4	> 13	> 15	Flocculated	> 0.1%
Sodic soil	Na salts (CO_3^{2-}, HCO_3)	> 8.5 to 10	< 4	> 13	> 15	Deflocculated	< 0.1%

Salinity distribution: A comparative study of global and Indian patterns

The global distribution of salt-affected soil, influenced by factors like climate, landscape, and human activities, is extensive and increasing. Despite the lack of precise statistics, approximately 1 billion hectares worldwide face salinity and sodicity stresses, with significant impacts on agricultural lands (Montanarella *et al*., 2015) [93]. Around 33% of irrigated agricultural lands and 20% of total cultivated lands globally face elevated salt concentrations (Shrivastava and Kumar, 2015) [138], leading to daily loss of about 2000 hectares of arable land (Zaman *et al*., 2018) [158] and an annual economic loss of approximately US $27.3 billion worldwide (Kumar and Sharma, 2020) [74]. Salinity issues span all climates, caused by both natural and human-induced processes, impacting soil water availability, osmotic pressure, and plant growth negatively. The Middle East leads with 189 million hectares of saline soils, followed by Australia and North America with 169 million and 144 million hectares, respectively. South Asia, including India, adds 52 million hectares. Globally, 85% of soils face slight to moderate salinity, while 15% pose significant challenges to crop production (Wicke *et al*., 2011) [153]. Secondary salinization affects 77 million hectares, mainly in cultivable and irrigated areas of countries like India, China, Pakistan, Iran, and Iraq. Primary salinization affects nearly 1 billion hectares worldwide (Cherlet *et al*., 2018) [27], with irrigation-induced salinization observed in countries such as Spain, Hungary, France, Southern Italy, and several Northern European countries (Daliakopoulos *et al*., 2016) [31].

In India alone, around 6.73 million hectares are currently affected, with projections indicating a rise to 20 million hectares by 2050. Saline soil covers about 2.956 million hectares, with the 3.77 million hectares being sodic (Kumar and Sharma, 2020) [74]. Gujarat, Uttar Pradesh, Maharashtra, West Bengal, and Rajasthan account for approximately 75% of India's salt-affected soil, totaling 4.03 million hectares (CSSRI-Karnal, 2015) [30]. This soil causes an annual loss of 16.84 million tons of agricultural production in India, with Uttar Pradesh and Gujarat most affected (Mandal *et al*., 2018) [88]. Increasing salinity also affects water quality, particularly in northwestern Indian states such as Punjab, Haryana, and Rajasthan. Globally, improper water management poses a significant risk of salinization in regions like Australia, the Middle East, the Mediterranean Basin, Northern Africa, and Central Asia (Cherlet *et al*., 2018) [27]. Future degradation of water quality is expected due to intensive irrigation practices and the strain on natural resources to meet the food demands of a growing population (Sharma and Singh, 2015) [163].

Physiological responses to salinity stress
Osmotic stress
Osmosis, the movement of water molecules across a selectively permeable membrane from an area of lower solute concentration (soil) to higher solute concentration (plant cell), is essential for maintaining cell turgor pressure and supporting cellular functions. Cell turgor pressure is the pressure exerted by the fluid (usually water) inside the central vacuole, resulting from the osmotic movement of water into the plant cell, maintains cell rigidity and shape by swelling the cell against the cell wall. This pressure is crucial for various physiological processes such as cell elongation, growth, and overall plant structure. Osmotic pressure or potential, driven by water molecules moving from a hypotonic (high OP, more water, less solutes) to a hypertonic solution (low OP, less water, more solutes) across a semi-permeable membrane, regulates water movement in the soil-plant system. Solutes in the soil solution, like minerals and salts, contribute to soil water's osmotic potential, determining the direction of water movement and facilitating water uptake by plant roots. Additionally, the osmotic potential of soil water influences the ability of plant roots to absorb water, crucial for maintaining the plant's water balance, turgor pressure, and overall functioning. This mechanism supports nutrient transport, metabolic processes like photosynthesis, and nutrient transportation through the xylem, highlighting the importance of osmotic potential in sustaining plant health and productivity.

Osmotic stress in plants refers to the physiological condition arises from an imbalance in water movement, causing damage or dysfunction in plant cells due to excessive water uptake or loss, affecting turgor pressure and overall plant health. This imbalance, often caused by high solute concentrations like salts in the soil solution, that leads to water being drawn out of plant cells, causing dehydration and hindered plant growth. Waterlogged soils can also induce osmotic stress by limiting oxygen availability, impairing root function. In saline soils, excess salt concentrations disrupt water potential, challenging water uptake by plant roots and impacting cellular processes, such as nutrient uptake and metabolism, ultimately affecting plant health and growth (Figure 6).

Ionic Stress
Ionic stress occurs when there is an excessive accumulation of specific ions, especially sodium (Na$^+$) and chloride (Cl$^-$), in plant tissues due to high soil salinity. When plants absorb water, they also take up these ions, leading to their accumulation in plant cells. The accumulation of sodium ions interferes with essential physiological processes, disrupts ion balance, and may cause toxicity, thereby affecting the structural integrity of cell membranes and disrupt enzyme activities, impacting overall plant health and growth (Figure 7).

Oxidative Stress
Oxidative stress occurs when there is an imbalance between the production of reactive oxygen species (ROS) and the ability of a plant to detoxify or repair the resulting damage. High salinity conditions can lead to the generation of reactive oxygen species (such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals) in plant cells. These ROS are highly reactive and can cause damage to cellular components, including lipids, proteins, and DNA.

Oxidative stress arises when the plant's antioxidant defense mechanisms are overwhelmed, leading to cellular damage and, in severe cases, cell death. Plants under salinity stress often need to manage oxidative stress to maintain cellular integrity and function (Figure 8).
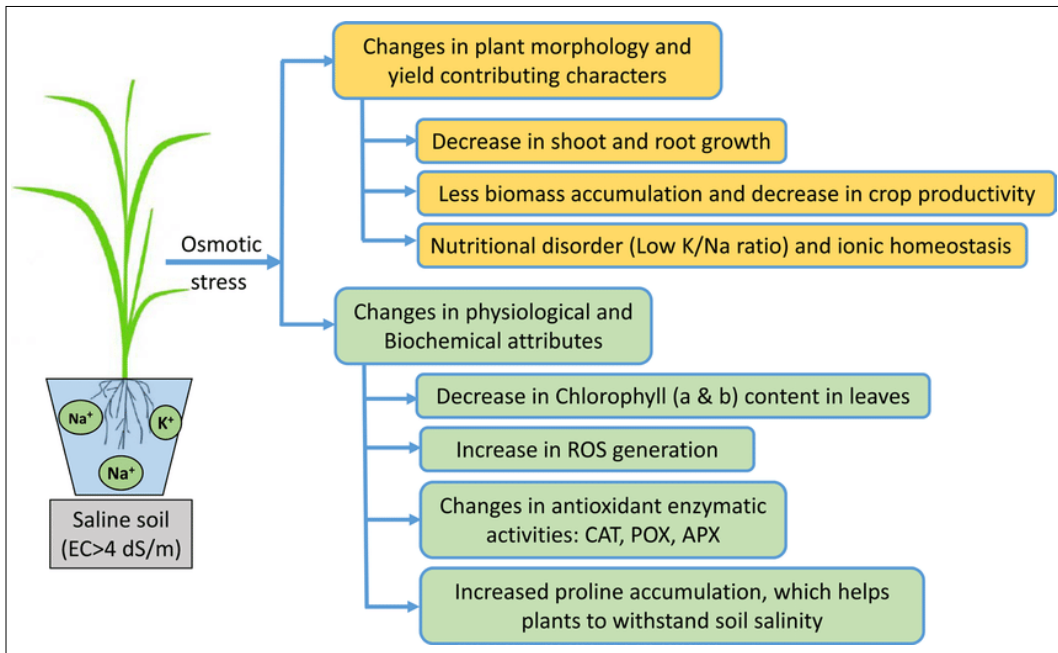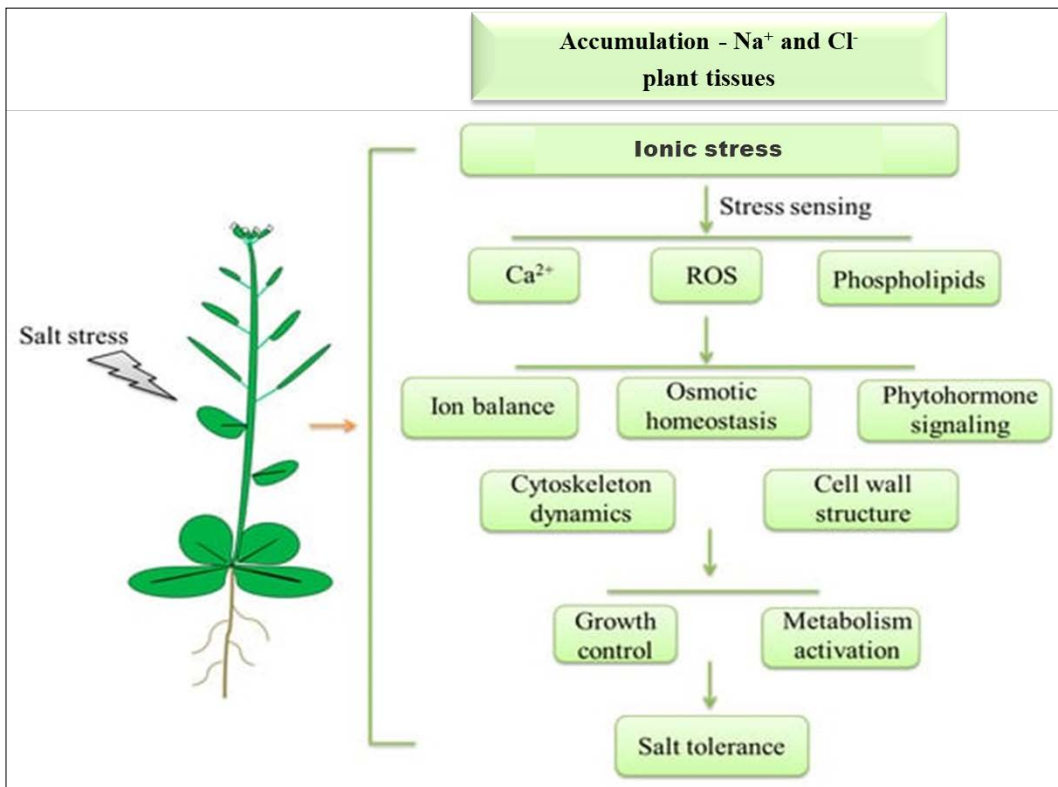

Fig 6: Salinity induced osmotic stress

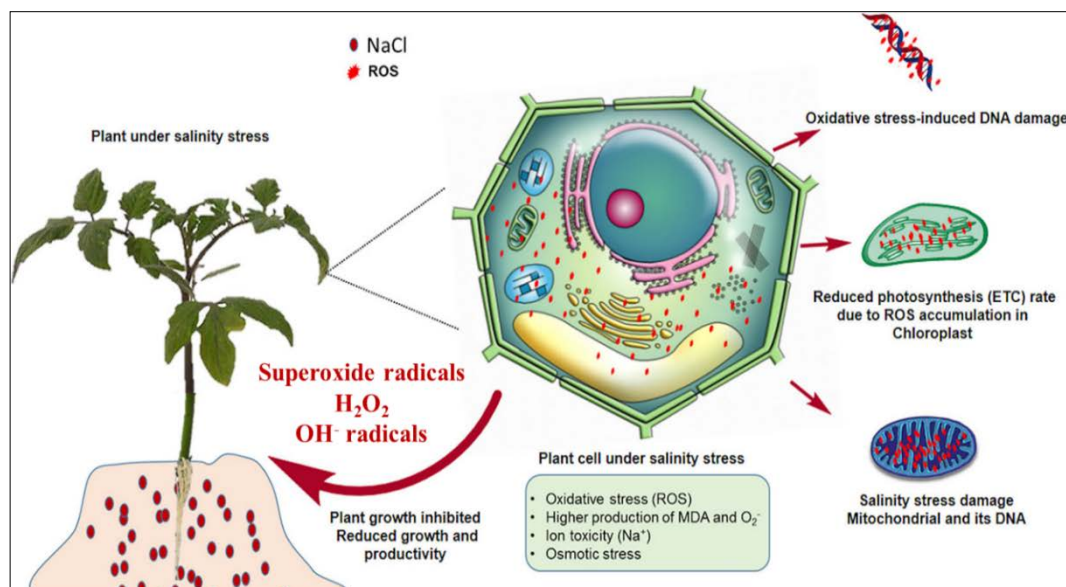**Fig 7:** Ionic stress caused due to accumulation of specific ions under high soil salinity

Fig 8: Oxidative stress induced by ROS imbalance under high soil salinity

Plant response to salt stress: Effect of salinity stress

Halophytes and glycophytes, categorized by their adaptive evolution, endure high salt concentrations and lack thereof, respectively. Most agricultural crops fall under glycophytes, raising concerns over decreased productivity due to salinity stress (Munns and Tester, 2008) [95]. Salinity not only affects soil properties and ecological balance but also leads to soil erosion and reduced economic returns, impacting all stages of plant development (Akbarimoghaddam *et al*., 2011) [6]. Distorted leaves, reduced respiration, and morphological changes are common responses, with salts at low concentrations acting as nutrients, though high levels disrupt nutrient equilibrium and uptake (Kumar and Verma, 2018) [72].

Elevated soil salt levels lead to reduced soil water potential and subsequent water scarcity, triggering varied plant responses such as decreased stomatal conductance due to production of abscisic acid and carbon assimilation, ultimately impacting yield (Roy *et al*., 2014) [121].

This salinity stress progresses through osmotic stress to ionic toxicity, disrupting physiological processes like nutrient balance, stomatal aperture, and photosynthetic activity (Shrivastava and Kumar, 2015) [138]. Soil salinization further hampers mineral nutrient absorption, particularly phosphorus, while excess Na^+ ions impede K^+ uptake crucial for plant growth (Assaha *et al*., 2017) [14]. Potassium, essential for various plant functions, becomes compromised under salinity stress, leading to oxidative damage and deleterious effects on plant growth and development (Erel *et al*., 2015) [36]. These multifaceted impacts extend to reproductive development stages, inhibiting crucial processes like microsporogenesis and fertilized embryo senescence (Ashraf, 2004) [13].

Salinity stress not only disrupts plant physiological processes but also affects photosynthesis, cell growth, and crucial molecular mechanisms (Flexas *et al*., 2007) [41]. Higher soil salinity levels inhibit seed germination and overall plant growth, posing challenges especially in arid and semiarid environments. The degree of salinity impact on plants depends on various factors, including species, genotype, growth phase, and the specific organ exposed to salt, highlighting the complex nature of plant-salinity interactions (Robin *et al*., 2016) [119].

Microbial Adaptation and Resilience to Salinity Stress: Halophiles and halotolerant microorganisms

Halophiles are microorganisms that thrive in environments with high salt concentrations. They have an obligate requirement on such conditions for their growth, and they possess mechanisms to withstand the challenges of high salinity while maintaining osmotic balance within their cells (Sharma and Arora, 2001) [133]. These organisms are found across the domains of Archaea, Bacteria, and Eukarya, and their classification based on their response to salt concentration is detailed in Table 3 (Arora *et al*., 2014) [11]. They are distributed in various environments such as arid regions, coastal areas, deep-sea locations, and artificial salters (Sharma and Arora, 2001) [133]. Additionally, halophiles can be found in association with the roots of halophytes, on the surfaces of macroalgae, and certain fish (Gontia-Mishra *at al*., 2017) [48]. Among the well-adapted and widely distributed halophilic microbes are archaeal species like Halobacterium, cyanobacteria such as *Aphanothece halophytica*, as well as various bacterial species including Bacillus, Micrococcus, Vibrio, and Halomonas (Mahadevaswamy and Nagaraju, 2018) [82]. Certain fungal strains like black yeast *Hortaea werneckii*, as well as species of *Aspergillus*, *Penicillium*, and *Alternaria*, are also known to thrive in high-salt environments (Al Tamie, 2016) [7]. India, with its coastline and salt lakes in Rajasthan and Orissa, boasts a rich biodiversity of halophiles.

In contrast, halotolerant microorganisms do not require high saline conditions for growth, but they can still thrive in such environments (Kumar and Verma, 2018) [72]. They exhibit tolerance to varying degrees of salt stress and include species like Bacillus, Pseudomonas, Halomonas, and Aeromonas (Ashraf *et al*., 2004) [13].

Table 3: Classification of halophiles based on their response to salt concentration

Sr. No.	Classification of halophiles	Concentration of salt (M)
1.	Non halophilic	< 0.2
2.	Slight halophiles	0.2-0.5
3.	Moderate halophiles	0.5-2.5
4.	Borderline extreme halophiles	1.5-4
5.	Extreme halophiles	2.5-5.2

Source: adapted from Arora *et al*., 2014 [11]

External stressors from the environment can induce fluctuations in microbial community dynamics, with the community's ability to resist such changes termed as resistance, and its capacity to return to its original state after stress removal termed as resilience (Kumar *et al*., 2020) [73]. Understanding these alterations is crucial due to their impact on rhizospheric diversity, affecting microbial attributes, community structure, and functions under salinity stresses. Functional diversity within a community can enable multiple processes to occur simultaneously at similar rates, with new salt-resistant bacteria potentially replacing pre-existing taxa and continuing similar metabolic functions, thereby enhancing soil health in saline environments and promoting plant growth (Kumawat *et al*., 2022) [75]. Various strategies employed by halo-tolerant bacteria to combat salinity stress include sodium ion export systems (Xu *et al*., 2022) [154], potassium/chloride ion accumulation instead of sodium ions (Zhang *et al*., 2018) [160], stabilization of cell walls through lacto-proteins by replacing glucose (Hamlet and Muller, 2013) [57], production of anionic phospholipase serves to shield microbial cells from elevated osmotic pressure and aids in preserving water within the plasma membrane and synthesis of compatible solutes assists in preserving the balance of electrolytes and water content within cells when exposed to high osmotic pressure. (Shivanand and Mugeraya, 2011) [137].

Diverse group of bacteria associated with plants can be classified into rhizospheric, phyllospheric, and endophytic groups. (Verma *et al*., 2017) [150]. The rhizosphere, influenced by root exudates, harbors the highest bacterial population, with organisms exhibiting flexible metabolic activities (Goswami *et al*., 2016) [50]. Root exudates coordinate signaling events, facilitating plant-microbe communication (Aamir *et al*., 2019) [1]. Root-secreted molecules like organic acids, phenols, and flavonoids act as chemical signals for various bacterial processes including quorum sensing, exopolysaccharide secretion, biofilm formation, and bacterial chemotaxis during root colonization (Ilangumaran and Smith, 2017) [64].

Bacteria thriving under saline conditions *viz*., Azospirillum, Microbacterium, and Rhizobium grow normally in the rhizospheric zone often secrete exopolysaccharides (EPS),

which enhance soil fertility by binding soil particles and increasing macropores, consequently promoting plant growth (Vimal *et al*., 2017) [151]. Plant growth-promoting rhizobacteria (PGPR) exhibit inherent traits such as survival in soil ecosystems, root colonization capabilities, and growth-promoting traits, making them valuable for sustainable agriculture (Ahemad and Khan, 2011) [4]. PGPR enhance plant growth through mechanisms like nutrient absorption enhancement, hormone production, mineral solubilization, siderophore production, ACC deaminase activity, and EPS secretion, thereby improving soil structure and fertility (Saghafi *et al*., 2019) [124].

The interaction between rhizobacteria and plant roots, facilitated by EPS secretion, aids in enduring adverse environmental conditions and enhancing plant growth. EPS-producing PGPR can improve soil properties, water retention, and nutrient uptake by plants under drought conditions, ultimately boosting plant growth and productivity (Rolli *et al*., 2015) [120]. Succinoglycan, an acidic type of EPS, holds commercial value for enhancing nodule formation in leguminous plants grown in saline soil, aligning with sustainable agriculture practices (Halder *et al*., 2017) [56]. Additionally, arbuscular mycorrhizal fungi (AMF) and PGPR can establish positive associations with plants, promoting soil aggregation and root-adhering soil, thereby facilitating nutrient and water uptake for plant growth (Rashid *et al*., 2016) [115]. Understanding the roles of halophilic bacteria and PGPR in mitigating salinity stress presents opportunities to enhance plant salt tolerance and improve agricultural practices under saline conditions. Further research is warranted to explore biological management strategies employing soil-inhabiting PGPR and halophilic microorganisms to optimize crop quality and yield in saline soils (Banerjee *et al*., 2019) [17].

Mechanisms of Salinity Tolerance by Salt Tolerant (ST) PGPRs

The mechanisms of salinity tolerance by Salt Tolerant Plant Growth Promoting Rhizobacteria (ST-PGPRs) are illustrated in Figure 9 and elaborated upon individually as follows.
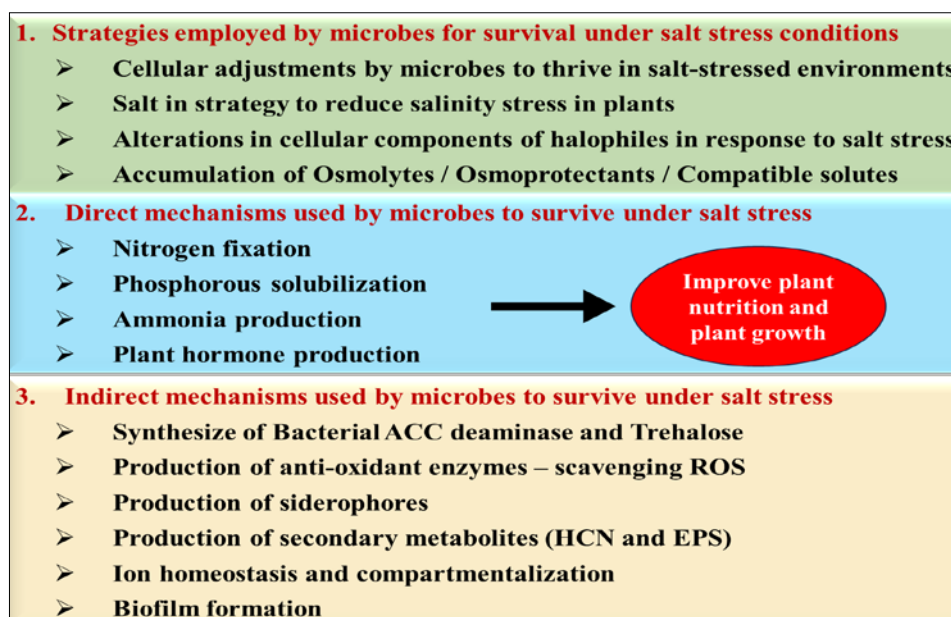

Fig 9: Mechanisms of salinity tolerance by St-PGPRs

Strategies employed by microbes for survival under salt stress conditions

Over the years, efforts have been made to comprehend the survival mechanisms of halophiles and halotolerant microbes in saline environments. These microorganisms adapt their intracellular processes in response to external conditions, as detailed in the following subheadings.

Cellular adjustments by microbes to thrive in salt-stressed environments

Salt-resistant microorganisms employ various cellular adaptations to thrive in saline environments, as depicted in Figure 10. For instance, to adapt osmotically, *Halobacillus halophilus* utilizes either organic / compatible solutes or inorganic ions (Gunde-Cimerman *et al*., 2018) [54]. In environments with high salt levels, halophiles might decrease their movement to save energy, potentially because the sodium-driven motors are less active. The genetic changes in the motility of *Halomonas beimenensis* was observed when exposed to 5% and 15% NaCl concentrations, showing reduced movement of cells and a decrease in the activity of genes responsible for flagellar movement in extremely salty conditions (Chen *et al*., 2017) [26]. Changes in the synthesis patterns of proteins and enzymes were investigated in Bacillus subtilis under osmotic stress conditions, revealing the activation of enzymes associated with modifying fatty acids and assimilating sulfate to repair FeS clusters in response to oxidative stress. Fungal cell walls undergo melanization during stress to prevent the loss of compatible solutes (Hoper *et al*., 2006) [61].

Although survival mechanisms are often alike across taxa, two primary strategies emerge (i) avoiding high saline conditions through overall cell structure modification and ion pumping, and (ii) acclimatizing proteins and enzymes to excessive solute ion concentrations (Ruppel *et al*., 2013) [122].
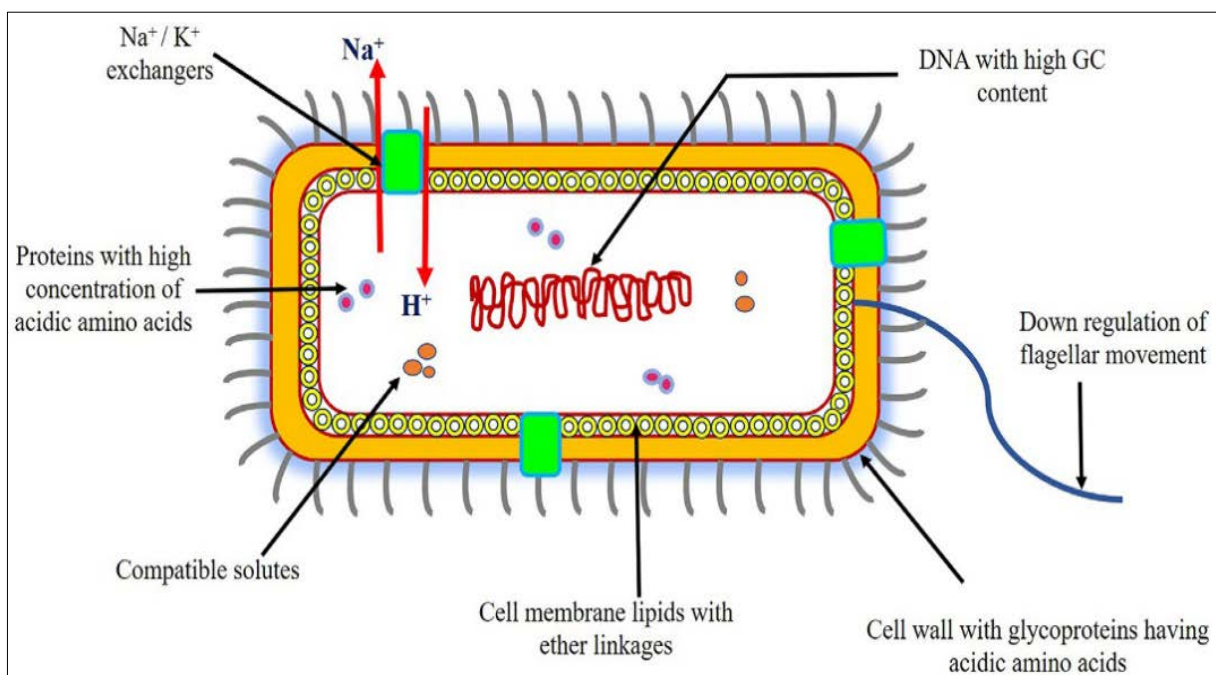

Fig 10: Cellular adjustments by microbes to thrive in salt-stressed environments (adapted from Kundu *et al*., 2022)

Salt in strategy to reduce salinity stress in plants

During instances of salt stress, plants employ strategies such as the removal of Na^+ and the uptake of K^+ to alleviate salinity stress. The influx of sodium ions into the cell adversely impacts the absorption of potassium by roots, leading to water deficiency, which manifests as detrimental effects such as abnormal transpiration rates, inhibited photosynthesis, reduced stomatal conductance, and decreased chlorophyll levels (Khan *et al*., 2019) [69]. In the "salt in" approach, cells accumulate a high concentration of salt, and this is regulated by ion pumps and protein transporters, which maintain the balance of K^+ and Na^+ within the cell, albeit at an energy cost, as illustrated in Figure 11 (Ali *et al*., 2016) [8]. To cope with high salt concentrations in the external environment, halophilic aerobic archaea and anaerobic halophilic bacteria utilize inorganic ions such as K^+, Mg^{2+}, and Na^+ (Salma and Mehnaz Samina, 2020) [126]. Certain bacteria species, including *Bacillus megaterium*, *Microbacterium oxydans*, *Arthrobacter woluwensis*, and *Arthrobacter aryabhattai*, are recognized for their ability to significantly improve the K^+/Na^+ ratio in plants while exhibiting characteristics that promote plant growth.
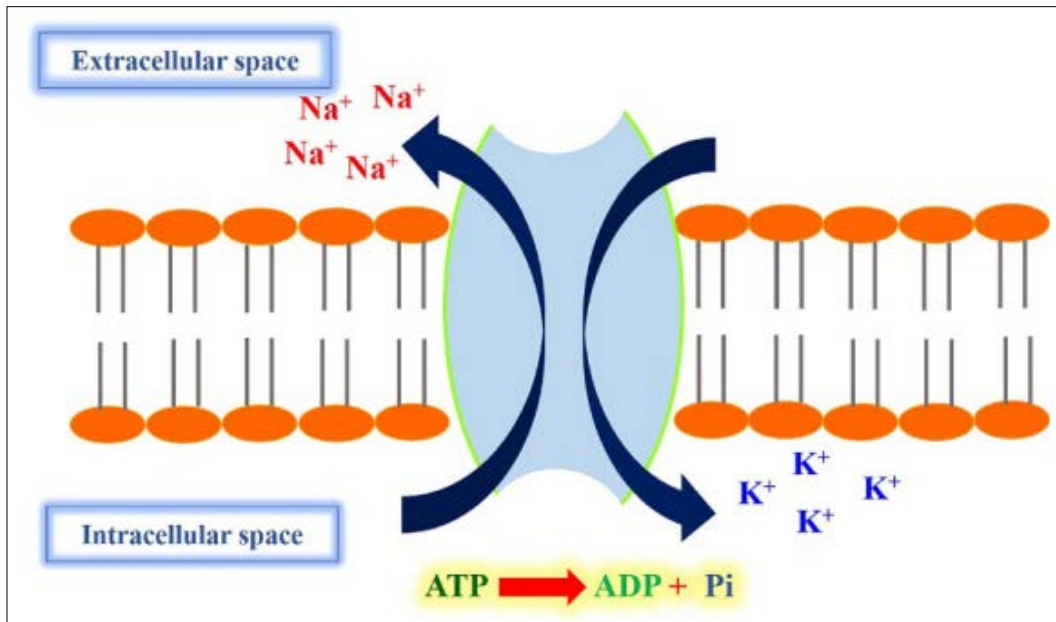
Fig 11: Schematic of sodium-potassium pump for plant salinity resistance (adapted from Kundu *et al*., 2022)

Alterations in cellular components of halophiles in response to salt stress

Proteins undergo denaturation and consequently lose stability, solubility, and crucially, functionality when exposed to salt stress (Sinha and Khare, 2014) [141]. Nevertheless, certain halophilic proteins thrive under saline conditions, suggesting a requirement for such environments. Halophilic proteins, in contrast to their non-halophilic counterparts, exhibit a higher proportion of acidic amino acids over basic ones. Research indicates that the presence of K^+ ions facilitate the formation of a hydration shell through ionic interactions with negatively charged proteins, thereby safeguarding their functionality. To ensure stability, the DNA of halophiles maintains a higher concentration of G + C, which enhances hydrogen bonding and stabilizes DNA in the high cationic environment within the cell. Microbial adaptations extend to lipid modifications to withstand osmotic stress. Halophilic archaea possess ether linkages in their membranes, which maintain membrane fluidity crucial for molecule transport across the membrane in hypersaline conditions (Litchfield, 1998) [79]. The cytoplasmic membrane, composed of such tetraether lipids, forms a robust barrier nearly impervious to protons.

Accumulation of osmolytes and compatible solutes

In hypersaline environments, halophilic bacteria and archaea have adapted through genetic and physiological modifications. These microorganisms face extreme hypersalinity, which causes water to move out of their cells along the osmotic gradient, leading to cytoplasm dehydration (Salma and Mehnaz Samina, 2020) [126]. To cope with these conditions, halophilic and halotolerant microorganisms, including bacteria, fungi, yeast, and algae, employ a compatible solute strategy. This strategy involves maintaining a low concentration of salts within the cell by synthesizing or absorbing compatible solutes while eliminating salts from the protoplasm. These compatible solutes, such as glycine, betaine, glutamine, proline, potassium, ectoine, and glutamic acid, are small, highly water-soluble organic compounds. They are either synthesized within the bacterial cell, absorbed from the medium, synthesized de novo, or derived from inorganic

solutes like Mg^{2+}, K^+, and Na^+. Glycine betaine, particularly the N-trimethyl derivative of glycine, stands out as the most effective compatible solute among osmolytes. It is accumulated intracellularly through synthesis, uptake, or both (Mahadevaswamy and Nagaraju, 2018) [82]. This accumulation of compatible solutes serves to maintain crucial processes for cell proliferation, including cell volume, turgor pressure, and electrolyte concentration (Roberts, 2005) [118]. Furthermore, these solutes play a role in stabilizing proteins under saline conditions (Litchfield, 1998) [79].

Plants accumulate organic osmolytes such as proline, glycine, betaine, polyamines, quaternary ammonium compounds, and other amino acids in response to various abiotic stresses. During salt stress, internal concentration of organic osmolytes may reach up to 1 M in certain halophilic bacteria and has a major role in destabilization of the double helix and lower the melting temperature of DNA. In moderately halophilic bacteria, salinity-induced expression of proline biosynthesis genes proH, proJ, and proA was reported at 2.5 M NaCl which led to the highest accumulation of proline (Saum and Müller, 2007) [129].

Osmotic adjustment is another salt tolerance adaptive mechanism acquired by plants to withstand salinity stress, which helps plants avoid ion toxicity and maintain water uptake by accumulating large quantities of osmolytes. These osmolytes could further be classified as organic solutes, also known as compatible solutes, and inorganic ions. Most of the osmolytes can function by balancing the osmotic potential of intracellular and extracellular ions in resistance to osmotic stresses. Inorganic ions, mainly Na^+, K^+, Ca^{2+}, and Cl, contribute to osmotic adjustment by ion transport processes carried out by ion antiporters and ion channels.

Compatible solutes like proline, glycine betaine, sugars, and polyols are crucial for enhancing plant salt tolerance. They protect cellular structures by regulating water influx and maintaining osmotic balance (Hasegawa *et al*., 2000) [59]. Intracellular proline accumulation serves as an adaptive mechanism to alleviate salinity stress, acting as an organic nitrogen reserve for stress recovery. In plants, pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase serves as key regulatory enzymes for higher

proline biosynthesis (Saxena *et al*., 2013) [130] Furthermore, glycine betaine is widely present ammonium compound in plants which maintains electrical neutrality over wide range of pH and acts as a nontoxic cellular osmolyte (Gadallah, 1999) [44]. It increases cell osmolarity during stress, mitigating its effects by adjusting osmotic balance, stabilizing proteins, and inhibiting ROS formation (Makela *et al*., 2000) [83]. This safeguards the photosynthetic apparatus from stress-induced damage. Studies have shown decrease in cellular sugar content with increasing salinity in plants (Kerepesi and Galiba, 2000) [68]. However, under salt stress, accumulations of sugars such as glucose, fructose, fructans, trehalose, and starch are reported (Parida *et al*., 2004) [107]. Certain carbohydrates primarily provide osmoprotection, store carbon, and scavenge ROS, aiding in plants' defense against salt stress.

Exploring Mechanisms for Plant Growth Promotion by Halophilic and Halotolerant Microorganisms
Reclamation of arable saline soil presents challenges due to its high salt concentration, rendering traditional physical and chemical processes ineffective and unsustainable. Cultivating salt-tolerant plant varieties has limited global reach, necessitating exploration of alternative approaches (Egamberdieva *et al*., 2019) [35]. A promising avenue involves harnessing bacterial and fungal communities around the plant root zone to stimulate growth under stress, thereby enhancing agricultural yield through various growth-promoting mechanisms (Otlewska *et al*., 2020) [103]. Microorganisms around the root zone benefit from organic carbon derived from shedding root cells and tissues, which constitutes a significant portion (85%) of total organic carbon. Root exudates provide essential nutrients acquired by chemotaxis, fostering a dense population of microbes in the rhizospheric soil. Examples of such bacteria include species of Azospirillum, Bacillus, and Pseudomonas spp. (Dimkpa *et al*., 2009) [32].
Isolating specific microbes and identifying their biochemical and molecular effects are crucial steps in this process (Khan *et al*., 2019) [69]. Beneficial bacteria that promote plant growth, when added to the soil or applied to plant parts, enhance growth effectively, particularly when used in a combined inoculation method (Kundan *et al*., 2015) [76]. Halotolerant bacteria, isolated and screened for NaCl tolerance levels, have shown adaptation to environmental conditions and synthesis of protective factors (Ramadoss *et al*., 2013) [114]. Various plant growth-promoting microbes, such as Flavobacterium, Bacillus, Pseudomonas, Rhizobium, and Acetobacter, continue to promote plant growth even in high saline environments. The utilization of salt-loving microbes in soil reclamation or enhancing crop yield under salt stress is based on the hypothesis that microbial activities will enhance the growth of resistant plant varieties and eliminate sodium from the soil vicinity (Arora *et al*., 2016) [10]. Salt-tolerant PGP bacteria emerge as significant alternatives to recover abandoned farmlands in arid and semiarid areas affected by salinity (Palacio-Rodrı´guez *et al*., 2017) [104]. These microbes not only support plant growth but also suppress harmful effects of biotic stress (Goswami *et al*., 2014) [49].
Screening of beneficial bacteria, especially from root-colonizing bacteria, and selecting appropriate strains is an effective strategy for selecting specific PGP bacteria and testing their efficacy on plants while monitoring the effects

(Kundan *et al*., 2015) [76]. Mechanisms employed by these bacteria include direct methods such as improving plant nutrition through solubilization of phosphate and micronutrients, nitrogen fixation, and production of phytoregulators like indole-3-acetic acid (IAA), cytokinin, and gibberellins. Indirect mechanisms involve the production of siderophores for iron acquisition, HCN production, and the enzyme ACC deaminase, which reduces ethylene levels in plants.

Direct mechanisms used by microbes to survive under salt stress
Nitrogen fixation
Nitrogen-fixing microorganisms play a crucial role in enhancing soil nitrogen levels and facilitating nitrogen provision to plants, thereby promoting plant growth and supporting seed germination (Mus *et al*., 2016) [96]. However, in saline soil, symbiotic nitrogen fixers like Rhizobium may not fully express their potential (Nogales *et al*., 2002) [100]. Additionally, under salt stress, legume roots often exhibit reduced nodules and inhibited root hair growth (Manchanda and Garg, 2008) [86]. In such environments, salt-tolerant nitrogen-fixing bacteria demonstrate higher efficiency compared to sensitive strains, utilizing mechanisms like osmolyte accumulation and EPS production for survival. Modified EPS and lipopolysaccharides (LPS) production may aid in root nodule formation (Nogales *et al*., 2002) [100].

Phosphate solubilization
Phosphorus (P) is vital for essential plant processes like photosynthesis, respiration, macromolecular biosynthesis, energy transfer, and signal transduction. When phosphate ions bind with calcium ions, they significantly reduce plant phosphate uptake (Mahadevaswamy and Nagaraju, 2018) [82]. Plant growth-promoting rhizobacteria (PGPR) produce compounds like organic acids, hydroxyl ions, protons, and CO_2, which help solubilize phosphorus, making it available to plants (Alori and Babalola, 2018) [9]. Utilizing such bacteria as bioinoculants in agriculture shows promise for enhancing P uptake by plants. Studies reveal that Bacillus genus P-solubilizing bacteria have regulatory mechanisms to cope with adverse environmental conditions such as humidity and temperature fluctuations, nutrient scarcity, oxidative stress, and salinity. Bacillus cereus, identified in saline environments, may serve such a protective role (Mohan *et al*., 2017) [92].

Ammonia production
Bacteria such as Bacillus and Pseudomonas species transform organic nitrogen residues into amino acids, which undergo ammonification to yield ammonia. This ammonia is utilized by various soil bacteria for cellular functions, including protein synthesis. *Nitrobacter* and *Nitrosomonas* species further convert the ammonia into nitrites, nitrates, and nitrogen gas. This process is crucial as ammonia production serves as a vital nitrogen source for the synthesis of biomolecules, alongside nitrogen fixation (Alori and Babalola, 2018) [9].

Production of plant hormones
Salt-tolerant microbes produce various plant hormones such as indole-3-acetic acid (IAA) and gibberellins, which have been shown to regulate plant physiology during salt stress

(Egamberdieva *et al*., 2019) [35]. IAA, an auxin-type hormone, plays a crucial role in seed germination and root development (Otlewska *et al*., 2020) [103]. Bacterial IAA facilitates nutrient uptake by regulating cell enlargement, division, and root architecture, leading to improved plant growth (Sharma *et al*., 2016) [134]. Additionally, it reduces the uptake of toxic ions, further enhancing plant growth. Halophilic bacteria, particularly Halomonas from Salicornia plants, have been identified as significant producers of IAA, contributing to plant growth promotion (Numan *et al*., 2018) [101]. Plant growth-promoting activity of Streptomyces under saline conditions, showed that salt stress increased the production of IAA (Sadeghi *et al*., 2012) [123].

Indirect mechanisms used by microbes to survive under salt stress
Production of 1-aminocyclopropane-1-carboxyate (ACC) deaminase
Ethylene, as a phytohormone, plays a crucial role in regulating physiological responses, germination, and seed dormancy breakage in higher plants (Zahir *et al*., 2019) [157]. It serves as a pivotal regulator in various developmental and growth processes while also mediating plant responses to environmental factors such as light, temperature, and nutrition, as well as different stress (Glick, 2012) [46]. However, excessive ethylene production under stressful conditions can be detrimental to seedlings, leading to plant death, originally characterizing it as a stress hormone (Raval and Desai, 2015) [116]. During salt stress, crops like rice, maize, wheat, and soybean exhibit increased ethylene emission, thereby shortening harvest shelf life (Pandey and Gupta, 2019) [105]. The rise in ethylene levels is attributed to increased activity of ACC oxidase (ACCO) and ACC synthase (ACCS) enzymes, in response to stress conditions such as salinity, flooding, drought and others, resulting in cell elongation inhibition, defoliation, and senescence (Shao *et al*., 2009) [131].
Several plant growth-promoting bacteria possessing ACC deaminase can mitigate ethylene levels under soil salinity and drought conditions. Chemical interventions like rhizobitoxin secreted by bacteria or use of cyclopropanes, as well as microbial approaches using ACC (1-aminocyclopropane-1-carboxylic acid) deaminase producing microbes, are employed to inhibit ethylene synthesis or accumulation (Sisler and Serek, 1997) [142]. The enzymatic activity of ACC deaminase in PGPB is fundamental in regulating ethylene levels by converting the ethylene precursor ACC into ammonia and α-ketobutyrate, which are utilized by bacteria for nutrition (Glick, 2014) [47]. These microbes when attached to seeds, prevent excessive ethylene levels that could impede initial root growth (Nadeem *et al*., 2010) [97]. PGPB synthesize and release indole acetic acid (IAA) in response to low levels of tryptophan in root exudates, promoting plant cell proliferation and elongation. However, excess IAA, which includes both endogenous plant IAA and that synthesized by bacteria, can trigger ethylene synthesis (Duca *et al*., 2014) [34]. Elevated ethylene levels inhibit IAA signal transduction, creating a negative feedback loop. ACC deaminase activity in PGPB reduces ethylene levels, relieving the inhibition of IAA signal transduction. This synergistic interaction between ACC deaminase and IAA is crucial for optimal PGPB function, facilitating plant growth even under ethylene-limited stress conditions (Malhotra and Srivastava, 2009) [84].

Studies have demonstrated that bacterial strains possessing ACC deaminase activity can improve plant resilience to salt stress, as evidenced in tomato seedlings (Mayak *et al*., 2004) [89], and the growth of red peppers was promoted by an ACC deaminase producing strain of *Pseudomonas frederiksbergensis* (Chatterjee *et al*., 2017) [23]. Various bacterial genera, including Bacillus, Rhodococcus, Alcaligenes, Variovorax, and Pseudomonas, exhibit ACC deaminase activity and can proliferate in soil (Dimkpa *et al*., 2009) [32].

Synthesis of Trehalose
Plant growth-promoting rhizobacteria utilize diverse mechanisms to protect plants from stresses like salinity and drought, causing dehydration and osmotic imbalance in plant cells (Forni *et al*., 2017) [43]. They synthesize osmolytes, aiding in osmotic adjustment and restoring cellular homeostasis (Orozco-Mosqueda *et al*., 2020) [102]. Studied osmolytes include amino acids, derivatives (e.g., glutamate, proline), peptides, sugars (e.g., sucrose, trehalose), and betaine (Vurukonda *et al*., 2016) [152]. Trehalose biosynthesis is widespread across various organisms, including archaea, fungi, plants, and bacteria. In bacteria five pathways of trehalose synthesis are known (Tournu *et al*., 2013) [145], while, fungi, plants, and certain animals utilize a single pathway (Avonce *et al*., 2006) [16].
Trehalose-producing bacteria demonstrate capability in alleviating multiple abiotic stresses, particularly enhancing plant growth under saline and drought conditions. Furthermore, trehalose accumulation in stressed cells aids in shielding cellular constituents from oxidative damage and thermal inactivation by maintaining partially folded polypeptide chains, facilitating their refolding by cellular chaperones (Benaroudj *et al*., 2001) [18]. Trehalose, a highly hydrophilic molecule existing as a nonreducing disaccharide, is formed by two α-glucose units connected by alpha-1-1-glucosidic bonds, rendering it resistant to acid hydrolysis even at elevated temperatures across a wide pH range (Iturriaga *et al*., 2009). Under freezing and dehydration conditions, trehalose forms hydrogen bonds with polar groups of surrounding molecules and membranes, potentially replacing lost water as cells dehydrate, thereby mitigating cell damage from salt and drought (Kosar *et al*., 2019) [71].
During osmotic stress, plants adjust cellular osmotic potential by synthesizing osmotic, osmoprotective, and compatible solutes like trehalose. This osmotic regulation can be triggered by trehalose-producing PGPB or by exogenous trehalose supplementation (Asaf *et al*., 2017) [12]. Under extreme dehydration, trehalose can crystallize, preserving biomolecules from denaturation while facilitating rehydration (Fernandez *et al*., 2010) [37]. Genetically modified plants carrying bacterial genes for trehalose synthesis exhibit maximum resistance to stress conditions. Bacterial strains overexpressing the trehalose gene, when bioinoculated in plants facing saline stress, display higher survival rates compared to non-inoculated plants. Additionally, highly nodulated *Phaseolus vulgaris* cultivars accumulate significant trehalose amounts in response to drought stress. Further exploration of trehalose's role and benefits to agricultural crops, particularly its response to abiotic stress and its interactions with other signaling pathways in plants, is recommended (Paul *et al*., 2020) [109].

Production of antioxidant enzymes

Reactive oxygen species (ROS) are produced as a natural byproduct of metabolic processes *i.e*., respiration and photosynthesis, in chloroplasts, mitochondria, peroxisomes, and other cell locations of plants. ROS are signalling molecules associated with plant development and defense at low levels. However, during salinity stress, an overabundance of ROS including free radicals (such as hydroxyl, superoxide, alkoxy radical, hydroxyl, alkoxyl, semiquinone, hydroperoxyl and carbonate), as well as non-radical molecules (like hypochlorous acid, singlet oxygen, hydroperoxides, hydrogen peroxide, hypoiodous oxide, hypobromous oxide and ozone) can lead to oxidative stress, causing damage to various cellular components including carbohydrates, lipids, proteins, DNA and other cell functions to impair plant growth. This imbalance can result in cellular damage, programmed cell death (PCD), and reduced plant productivity (Hasanuzzaman *et al*., 2020) [58]. To counteract this, plants employ antioxidant enzymes such as ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferases (GST), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR),

which scavenge ROS and maintain them at manageable levels. Certain bacteria-produced enzymes, like catalase and superoxide dismutase, also play a protective role against ROS during stressful conditions.

SOD converts superoxide radicals to hydrogen peroxide (H_2O_2), while CAT breaks down H_2O_2 into water (H_2O) and oxygen (O_2). Additionally, APX contributes to the breakdown of peroxide produced by SOD (Habib *et al*., 2016) [55]. Studies have shown increased SOD and CAT activities in olive leaves treated with high levels of salt (200mM NaCl), indicating the crucial role of antioxidants under salt stress (Valderrama *et al*., 2006) [149]. Among the nonenzymatic, low molecular antioxidants, including phenolics, flavonoids, tocopherols, phenols, free proline, ascorbate and glutathione, are among those that protect plants from oxidative stress (Symes *et al*., 2018) [143]. In a study by Habib *et al.* (2016) [55], significant CAT activity was observed in salt-stressed plants inoculated with plant growth-promoting rhizobacteria (PGPR) compared to control okra plants. Moreover, chlorophyll content was higher in plants inoculated with ACC deaminase-producing PGPR, suggesting enhanced ROS scavenging enzyme activity and adaptation to saline conditions.
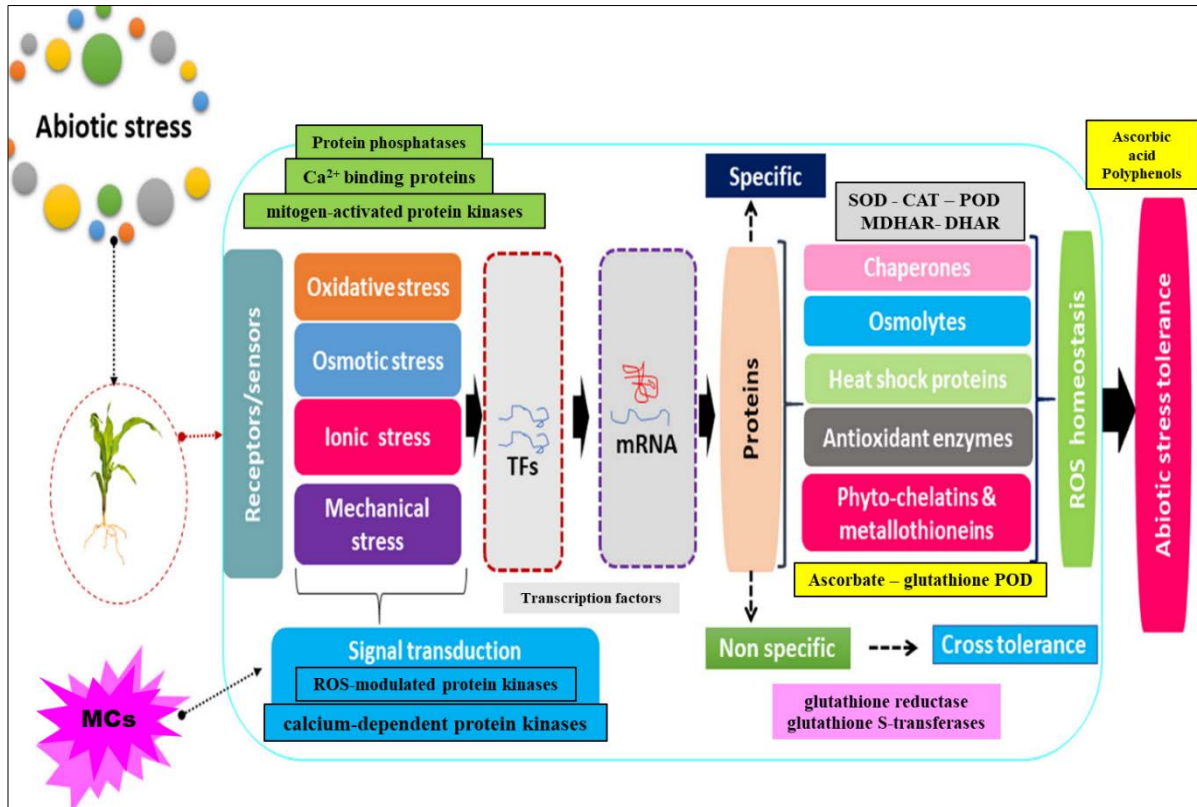

Fig 12: Microbes with a variety of defense mechanisms in plants under abiotic stress

As showed in the figure 12, early prevalence of stress sensing via receptors/sensors cascades the downstream stress response by ROS, CaBP (Ca²⁺ binding proteins), and plant hormones. Signal extension and transduction is carried out by secondary messengers, *i.e*., MAPKs (mitogen-activated protein kinases), PKs (ROS-modulated protein kinases), PPs (protein phosphatases), CDPKs (calcium-dependent protein kinases). Signalling causes various regulation of transcription factors (TFs) and stress-responsive genes. Control of TFs and genes linked with

physiological, biochemical, and molecular responses may adjust to fine-tune enhanced stress resistance capacity. Enhancing functional and structural protective mechanisms like antioxidants and osmolytes can boost plants' resistance to stress. Antioxidative enzymes and low-molecular-weight metabolites scavenge ROS, mitigating oxidative stress. Elevated levels of antioxidants facilitate the production of compounds like ascorbic acid and polyphenols, which may neutralize ROS to reduce oxidative stress. These enzymes and metabolites work together to protect plants from

oxidative stress and maintain cellular redox homeostasis, thereby contributing to the overall defence mechanism against ROS-induced damage in plants.

Production of siderophores

Several enzymes crucial for respiration, photosynthesis, and nitrogen fixation rely on the micronutrient iron (Fe) (Abbas *et al*., 2015) [2]. Salinity stress diminishes Fe availability for plants by downregulating Fe transporters (Ferreira *et al*., 2019) [38]. However, plant growth-promoting bacteria that produce siderophores have been shown to enhance plant health. Bacterial siderophores serve to hinder or reduce the proliferation of pathogens by depriving them of access to iron, thereby impeding their growth.

Siderophores are small peptide molecules capable of binding ferric ions, possess side chains and functional groups with high specificity ligands for ferric ions (Alori and Babalola, 2018) [9]. These low molecular-weight chelating agents exhibit a strong affinity for ferric iron and are synthesized by microorganisms in iron-restricted conditions. They play a crucial role in sequestering and transporting iron in microbial species, effectively scavenging Fe and forming complexes with other essential elements such as Mo, Mn, Co, and Ni in the environment, thereby making them available for microbial cells.

Various bacteria and fungi produce siderophores strong enough to remove iron from host-binding proteins. In Gram-negative bacteria, outer membrane protein receptors detect specific Fe_3^+ siderophore complexes on the cell surface under conditions of iron deficiency, demonstrating the widespread importance and functionality of siderophores in microbial systems. Many plants do grow at a low iron level around their root zone and hence the depletion of iron due to bacterial siderophores does not hamper plant growth (Numan *et al*., 2018) [101]. Hence, siderophore production is an important trait as plants may take up Fe_3^+ siderophores directly or by ligand exchange. Observations indicate that the production of siderophores plays a crucial role in enhancing plant growth, with an observed rise in biosynthesis in the presence of NaCl (Sadeghi *et al*., 2012) [123]. PGPRs have been discovered to mitigate salt stress in tomato plants, as demonstrated by the study of siderophore production at 6% NaCl by PGPRs (Tank and Saraf, 2010) [144].

Production of Hydrogen cyanide (HCN)

Hydrogen cyanide (HCN), primarily produced by Pseudomonas and Bacillus species, serves as a secondary metabolite with potent antimicrobial properties against pathogens (Kundan *et al*., 2015) [76]. Additionally, HCN-producing bacteria facilitate the mobilization of elements from mineralized rocks. In acidic soils, phosphates bind with iron or aluminum, whereas in basic soils, they form complexes with calcium. Biogenic HCN in acidic soils interacts with iron, effectively sequestering it and enhancing phosphate availability, thus promoting plant growth (Rijavec and Lapanje, 2017) [117]. Additionally, HCN disrupts the electron transport chain, leading to cellular energy deprivation and ultimately cell death.

Production of Exopolysaccharide

Production of exopolysaccharide (EPS) or surface polysaccharides is a common characteristic observed in certain rhizosphere bacteria. While the type and quantity of EPS may vary among different strains of ST-PGPR, they typically produce ample EPS under adverse conditions (Khan and Bano, 2019) [70]. EPS acts as a protective barrier around roots, facilitating plant growth during periods of high salinity stress (Vaishnav *et al*., 2016) [148]. Halophiles and halotolerant bacteria employ distinct metabolic pathways to synthesize polysaccharides, which help alleviate salt stress by sequestering Na^+ ions and forming a protective layer around plant roots, thereby reducing their uptake (Shin *et al*., 2016) [135]. Consequently, an increased presence of EPS-producing bacteria near the roots may decrease Na^+ uptake by plants, aiding them in coping with saline stress.

The introduction of EPS-producing ST-PGPR via inoculation has also demonstrated beneficial effects on the uptake of K^+, Na^+, and Ca^{2+} in plants. It was observed that EPS-producing ST-PGPR strains, such as *Halomonas variabilis* (HT_1) and P. *rifietoensis* (RT_4), enhanced chickpea growth and soil structure stabilization under saline conditions. Additionally, EPS presence in biofilms enhances root colonization by ST-PGPR. Regarding yield enhancement, EPS-producing ST-PGPR play a crucial role as priming agents for seeds, aiding in improved germination (Qurashi and Sabri 2012a) [112]. It was demonstrated that salt-tolerant EPS-producing strains of *Bacillus subtilis* subsp. *inaquosorum* and *Marinobacter lipolyticus* SM19 mitigated the adverse effects of salinity and drought stresses in wheat. Recently, the potential role of EPS-producing, salt-tolerant *Pseudomonas* PS01 strain in regulating stress tolerance-related genes was highlighted in *Arabidopsis thaliana*. Additionally, up-regulation of the LOX2 gene was observed, which is involved in jasmonic acid (JA) synthesis, a key stress regulator in plants under salt stress conditions. The bacterial EPS provided additional benefits for survival under salt stress by aiding in JA accumulation (Qurashi and Sabri, 2012b) [113].

Experiments have been conducted to elucidate the role of exopolysaccharide producing bacteria from *Bacillus* and *Aeromonas* genera, *Pseudomonas* and *Microbacterium* species in wheat seedlings exposed to moderately saline conditions. Salt-tolerant Azospirillum species producing EPS was also found to promote plant growth, stimulating Na^+ uptake by roots and its transportation to shoots. This resulted in an increased K^+: Na^+ ratio and selectivity in roots, with favoured K^+ transport from roots to shoots (Ashraf *et al*., 2004) [13]. Lower Na+ levels were observed in roots and shoots compared to rhizospheric soil, indicating that EPS-producing bacteria inhibited Na^+ uptake. Therefore, salt-tolerant EPS-producing bacteria could assist salt-susceptible plants in surviving salt stress by restricting Na^+ influx. It was discovered that a consortium of EPS-producing Enterococcus and Bacillus species decreased plant cation uptake in saline soil. Consequently, an increase in the population of EPS-forming bacteria near the roots may reduce the available Na^+ content for plants (Upadhyay *et al*., 2011) [147].

Nitric oxide (NO) roles in salt tolerance

Nitric oxide (NO) is a gaseous compound recognized for its volatility and its role in various growth and developmental processes, including respiration, root growth, and stomatal closure. Mishra *et al.* (2011) [91] have identified the positive impacts of nitric oxide on salinity tolerance, attributing them to its antioxidant properties and its capacity to regulate the

detoxification of reactive oxygen species. Application of exogenous nitric oxide under conditions of salt stress has been linked to a reduction in lipid peroxidation levels (Nalousi *et al*., 2012) [98] and an enhancement in plant growth, associated with enhanced activity of antioxidant enzymes such as ascorbate peroxidase, catalase, superoxide dismutase, glutathione reductase, and glutathione peroxidase (Zhao *et al*., 2004) [162].

The role of nitric oxide in salinity tolerance extends to its influence on plasma membrane H^+-ATPase and the Na^+/K^+ ratio (Crawford, 2006) [29]. Nitric oxide stimulates H^+-ATPase, establishing a proton (H^+) gradient that facilitates Na^+/H^+ exchange, thereby aiding in K^+ and Na^+ homeostasis (Zhang *et al*., 2006) [161]. Furthermore, it has been shown that salt stress-induced production of hydrogen peroxide activates plasma membrane H^+-ATPase, leading to an elevated K^+/Na^+ ratio that supports alleviation of NaCl stress. Ahmad *et al*. (2016) [5] demonstrated that nitric oxide alleviates salt stress by regulating osmolyte levels and antioxidant enzyme activities in chickpea. Additionally, salt resistance was reported in *Populus euphratica* due to involvement of H_2O_2 and nitric oxide (Zhang *et al*., 2007) [159].

Hormonal regulations of salt tolerance
During salt stress, various signaling pathways, including phospholipids, hormonal signaling, and calcium ions (Ca^{2+}), coordinate to regulate osmotic adjustments crucial for plant growth. ABA accumulation mitigates salinity effects by storing K^+, Ca^{2+}, and compatible solutes in root vacuoles, counteracting Na^+ and Cl^- uptake (Chen *et al*., 2001) [25]. Polyamines contribute to cellular osmoregulation either through direct binding or via PA-induced signaling molecules like ROS and NO thus indirectly modulating ion channels and membrane depolarization (Singh *et al*., 2018) [139-140]. Several studies suggest that auxin signaling pathways respond to salinity stress, with elevated auxin concentrations significantly impacting root architecture by altering auxin accumulation and distribution (Petersson *et al*., 2009) [110]. Overexpression of auxin biosynthetic-related YUCCA3 leads to hypersensitivity to salt stress due to increased auxin levels (Jung and Park, 2011) [67]. Cytokinins enhance abiotic stress tolerance, potentially counteracting ABA's effects on salt tolerance (Javid *et al*., 2011) [65]. Salt-tolerant cultivars exhibit elevated endogenous jasmonic acid (JA) levels, which mitigate salt-induced defects in seedling development and photosynthetic activity (Yoon *et al*., 2009) [156]. Evidence suggests crosstalk between ABA and JA in regulating salt stress (Shinozaki and Yamaguchi-Shinozaki, 2007) [136]. Recent molecular investigations highlight the positive role of brassinosteroids (BR) in bolstering salt and drought tolerance, interacting with auxin, ABA, and SA (Manavalan *et al*., 2012) [85]. Gibberellic acid (GA) contributes to salinity tolerance by regulating plant growth via DELLA proteins-mediated growth retardation (Achard *et al*., 2008) [3]. Ethylene is biologically linked to salt stress signaling, with the ethylene-insensitive mutant etr1-1 displaying enhanced sensitivity to salt stress (Cao *et al*., 2008) [21].

Ion homeostasis and compartmentalization
Ion homeostasis is the maintenance of balanced internal conditions regarding ion concentrations, including sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), and chloride (Cl^-),

within cells and organisms. This balance is vital for proper cellular function and overall physiological health.

In soil, sodium chloride (NaCl) is the predominant salt. Typically, sodium ions enter the cytoplasm and then move to the vacuole via a Na^+/H^+ antiporter. Vacuolar membranes contain two types of H^+ pumps, of this V-ATPase being the primary pump in plant cells, contributing to ion homeostasis. The salt overly sensitive (SOS) stress signaling pathway plays a significant role in ion homeostasis and salt tolerance (Atienza *et al*., 2007) [15]. This pathway involves three key proteins *viz*., SOS_1, SOS_2, and SOS_3. SOS_1, a plasma membrane Na^+/H^+ antiporter, regulates cellular Na^+ efflux and guide transport of Na^+ from roots to shoots, enhancing salt tolerance when overexpressed in plants. SOS_2, a serine/threonine protein kinase encoded with N-terminal catalytic domain and a C-terminal regulatory domain, is activated by salt stress via Ca_2^+ signaling (Liu *et al*., 2000) [80]. SOS_3, a myristoylated Ca_2^+-binding protein encoded with N-terminus myristoylation site, interacts with SOS_2, leading to SOS_1 phosphorylation and increased Na^+ efflux, thus reducing Na^+ toxicity.

The C-terminal region of the SOS_2 protein contains a 21-amino acid sequence called the FISL motif (NAF domain). This motif serves as a binding site for the Ca_2^+-binding SOS_3 protein. This interaction (SOS_3-SOS_2) activates the kinase, leading to the phosphorylation of the SOS_1 protein, which enhances its transport function. As a result, the increase in Na^+ concentration prompts a rise in intracellular Ca^{2+} levels, facilitating Ca^{2+} binding to SOS_3. Ca^{2+} also helps regulate intracellular Na^+ levels alongside SOS proteins. Consequently, SOS_3 interacts with and activates SOS_2, forming a complex that phosphorylates SOS_1, leading to increased Na^+ efflux and a reduction in Na^+ toxicity.

Cells regulate ion movement (influx and efflux) across membranes using channels, transporters, and pumps. Proper ion balance is critical for various cellular functions, including maintaining membrane potential, signal transmission, muscle contraction, nerve impulses, and enzyme activity. In multicellular organisms, maintaining ion concentrations is crucial for fluid and tissue stability. Disruptions in ion balance can lead to cellular dysfunction, affecting physiological processes and potentially causing health problems or diseases.

Biofilm formation and phases in biofilm formation
A biofilm is described as a community of microbes bind to either inert or living surfaces, enclosed within a matrix primarily composed of polysaccharides, which is self-produced by the microorganisms and referred to as the extracellular matrix or extracellular polymeric substance (EPS). This matrix includes various macromolecules such as mono and polysaccharides, lipids, extracellular DNA, proteins, minerals, and water, serving as an adhesive promoting cell-cell and cell-substrate interactions (Santos *et al*., 2018) [127]. The concept of microorganisms living collectively was initially observed on tooth surfaces in studies conducted by Antonie van Leeuwenhoek (1632-1723), who termed this organized microbial existence as "microbial aggregation" (Santos *et al*., 2018) [127]. The term "biofilm" was later coined by Bill Costerton in 1978 (Berlanga and Guerrero, 2016) [16]. Biofilms are now recognized as one of the most efficient and prevalent life forms on Earth (Flemming *et al*., 2016) [40].

Biofilms can consist of single microbial species or multiple microbial species (Msarah *et al.*, 2018) [94], forming either single-layer or multilayered structures (Pandit *et al.*, 2020) [106]. They display both elastic (reversible) and viscous (irreversible) responses, largely influenced by external forces acting on the matrix. With cell densities ranging from 10^8 to 10^{11} cells per gram of wet weight, biofilms are complex systems comprising diverse microbial species undergoing differentiation based on local conditions, triggering the expression of specific genes and proteins at distinct stages, leading to heterogeneity within the biofilms. Heterogeneity can arise from gradients of electron acceptors, nutrients, waste products, or mutations, resulting in phenotypic and genotypic variants (McDougald *et al.*, 2012) [90]. The presence of diverse microorganisms from different genera, species, and environments contributes to the characteristic chemical composition, structure, and 3D assemblies of biofilms, where complex interactions such as competition and synergism influence construction and functions within multispecies biofilms.

Various factors including hydrodynamic conditions, nutrient availability, cell motility, cell-to-cell communication, extracellular matrix, and proteins influence the structural design of biofilms (Flemming and Wingender, 2010) [39]. Microbes tend to form communities in harsh environments rather than enduring stress individually, facilitating a collective stress response and ensuring viability by performing intricate functions akin to different life processes. Biofilm formation in nature is prompted by environmental stresses unfavourable for microorganisms, leading to essential modifications in metabolic pathways such as regulatory changes in gene expression, rearrangement of microbial cells, cell surface alterations, and adjustments in nutrient uptake behaviours to survive in altered environments (Bridier *et al.*, 2011) [20]. Bacteria typically form biofilms under conditions of nutrient scarcity, as high nutrient conditions often result in unsuccessful biofilm formation or the formation of loose flocs easily dislodged by fluid stress, illustrating the pivotal role of environmental factors in determining whether cells adopt a planktonic or surface-bound biofilm lifestyle (Petrova and Sauer, 2012) [111]. Previous investigations have shown that 99% of bacteria in nature prefer attaching to surfaces via biofilm formation, providing protection against antimicrobial agents.

The process of biofilm formation is a complex, multistep event that unfolds in a sequential and coordinated fashion, ultimately yielding a 3D architectural arrangement. This structure facilitates the creation of water channels, fostering the exchange of nutrients or gases crucial for microbial cell proliferation and maturation (Donlan, 2002) [33]. Initially, the biofilm harbours a substantial population of motile cells, yet as the formation progresses, the majority of these cells transition into matrix-producing cells. Additionally, a subset of matrix-producing cells differentiates into sporulating cells (Lo´pez, Vlamakis, and Kolter, 2010) [81]. Within cells, cyclic di-GMP (c-di-GMP) acts as a messenger, modulating the transition of cells from the confined biofilm environment to free-living cells in response to diverse environmental cues and intercellular interactions. Elevated levels of c-di-GMP promote biofilm formation while suppressing bacterial motility. The concentration of c-di-GMP is finely tuned in reaction to external stimuli sensed by various detection systems (Chang, 2018) [22]. Biofilm formation commences with the adsorption of molecules onto the surface, followed by bacterial attachment and extracellular polymeric substance (EPS) release, ultimately culminating in colony establishment and biofilm maturation (Sharma *et al.*, 2019) [132]. The successive phases leading to biofilm formation are illustrated in Figure 13.
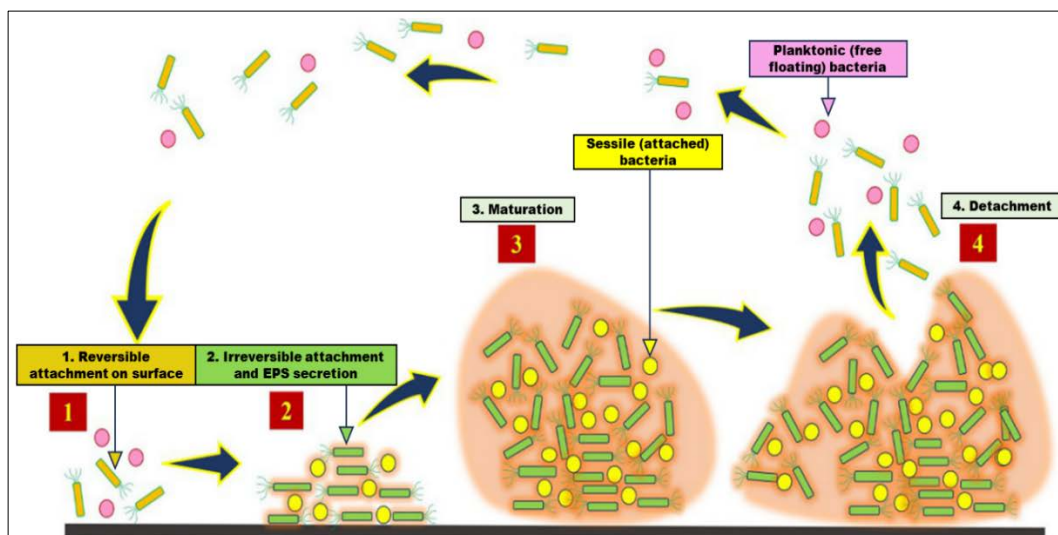

Fig 9: Phases of biofilm development

During Phase 1, microbial cells adhere reversibly to the surface, influenced by environmental factors like pH, temperature, nutrients, and oxygen levels (Nithya *et al.*, 2020) [99]. Some cells detach due to flexible attachment, marking the shift from planktonic to biofilm life. Initially, bacteria loosely attach and move swiftly across the surface through vibrating and spinning motions, aided by twitching motility and Brownian motion, facilitated by pili. Flagella and pili are crucial for establishing initial physical contact with the surface, by mitigating the hydrodynamic boundary layer and reducing repulsive forces between cells and the surface (Petrova and Sauer, 2012) [111]. Following adherence to the surface in Phase 2, microbial cells commence multiplication and intra-cellular communication facilitated by various signal molecules. Throughout this phase, numerous bacteria generate bis-(30 -50)-cyclic dimeric

guanosine monophosphate (c-di-GMP), an intracellular messenger, to regulate EPS secretion. EPS, in conjunction with surface proteins like SadB or LapA, facilitates the irreversible adhesion of cells. EPS's function at this juncture is to assimilate free-living cells and nutrients, thereby restricting cellular movement. Post irreversible adhesion, cells aggregate into microcolonies, initiating cellular proliferation within the previously attached cells on the surface. These microcolonies proliferate and produce EPS (Toyofuku *et al*., 2016) [146]. Phase 3 represents the maturation stage of biofilms, wherein cells arrange into layers with a thickness potentially exceeding 10 mm. Phase 4 marks the continued maturation stage, where the thickness extends to 100 mm or more. In Phase 5, the final stage involves the detachment of a few cells from the biofilm. Some cells disperse from the mature biofilm into the surrounding environment, a process that can be either active or passive. Active dispersal occurs in response to environmental changes like temperature fluctuations or oxygen depletion. During active dispersal, genes responsible for extracellular polymeric substance production and attachment are downregulated, while those involved in cell motility and EPS degradation are upregulated. Passive dispersal typically occurs due to physical factors such as shear stress from liquid flow. This dispersal process provides an opportunity to initiate the cycle of biofilm formation on a new surface (Sharma *et al*., 2019) [132].

New biofilm formation arises from the mature, established biofilm through various mechanisms including desorption, detachment, and dispersion. Desorption involves the passive release of microbial cells from the biofilm into the surrounding environment, typically observed during initial biofilm development. In contrast, detachment occurs due to external forces such as erosion or abrasion. Occasionally, regulatory systems induce physiological changes in the biofilm, facilitating the active release of cells from it (Petrova and Sauer, 2016) [111]. Bacterial biofilms exhibit diverse morphologies, ranging from thin, flat structures to large, tower-like 3D formations. They vary in complexity and physiological makeup, with multilayered cells compacting the biofilm structure and hindering access to biocidal molecules (Bridier *et al*., 2011) [20]. The diverse morphology aims to trap cells within the biofilm, fostering mixed-species colonies and providing a heterogeneous habitat (Flemming and Wingender, 2010) [39].

Microbial cells within biofilms express different phenotypes compared to their free-living counterparts, showing distinct gene transcription, translation, expression, and growth rates (Donlan, 2002) [33]. These cells also exhibit altered metabolic activities, including increased extracellular polymeric substance (EPS) production, reduced growth rates, and modulation of gene expression related to biofilm formation (Sharma *et al*., 2019) [132]. To adapt to changing environments, microbial cells in biofilms engage in lateral gene transfer, exchanging plasmids and transposons to acquire specific phenotypic traits such as antimicrobial resistance or virulence expression (Bridier *et al*., 2011) [20]. Furthermore, biofilm-associated cells demonstrate synchronization, association, and information exchange (Pandit *et al*., 2020) [106]. Although not essential for bacterial survival, biofilms enhance the likelihood of survival and proliferation under adverse conditions. Studies have shown that biofilms provide protection against various stressors including high pressure, UV radiation, nutrient scarcity,

extreme pH and temperature, salinity stress, and antibiotics (Yin *et al*., 2019) [155]. This protection primarily stems from EPS, which shields microbial cells from physical, chemical, and biological agents such as desiccation, UV radiation, oxidizing agents, biocides, antibiotics, metallic cations, and certain protozoan grazers, as well as host immune responses. These differences arise from the high cell density, nutrient scarcity, and high osmolarity of the microenvironment in which biofilm-associated organisms thrive (Sharma *et al*., 2019) [132].

Conclusion
In conclusion, this review emphasizes the critical role of soil microbiomes in maintaining soil health and enhancing agricultural productivity, particularly in saline environments. The study elucidates the intricate adaptation mechanisms of halophiles and salt tolerant plant growth promoting rhizobacteria (ST-PGPRs) to high salt concentrations, offering promising avenues for enhancing plant resilience and productivity. These microorganisms employ diverse strategies such as osmolyte accumulation, salt-in mechanisms, and synthesis of growth-promoting compounds like indole-3-acetic acid and ACC deaminase. Additionally, microbial-mediated processes including nitrogen fixation, phosphorous solubilization, and siderophore production contribute to nutrient cycling and antioxidant defense in plants under salinity stress. Innovative approaches such as chemical interventions and microbial-based strategies targeting ethylene regulation and trehalose production demonstrate potential in alleviating multiple abiotic stresses. Furthermore, the importance of antioxidant enzymes and biofilm formation in enhancing soil health and agricultural productivity in salt-affected regions cannot be overstated. Understanding ion homeostasis and signaling pathways involved, such as the SOS stress signaling pathway, provides further insights into plant adaptation to saline conditions. Incorporating these microbial strategies into agricultural practices holds significant promise for mitigating the detrimental effects of salinity stress on crop productivity and soil health, thereby fostering sustainable agricultural systems in salt-affected regions worldwide. By leveraging these microbial strategies, we can develop scientifically informed and sustainable agricultural practices, contributing to global food security and ecosystem resilience.

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