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Plants take action to mitigate salt stress: Ask microbe for help, phytohormones, and genetic approaches

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Abstract: Global agriculture is a pivotal activity performed by various communities worldwide to produce essential human food needs. Plant productivity is limited by several factors, such as salinity, water scarcity, and heat stress. Salinity significantly causes short or long-term impacts on the plant photosynthesis mechanisms by reducing the photosynthetic rate of CO_2 assimilation and limiting the stomatal conductance. Moreover, disturbing the plant water status imbalance causes plant growth inhibition. Up-regulation of several plant phytohormones occurs in response to increasing soil salt concentration. In addition, there are different physiological and biochemical mechanisms of salt tolerance, including ion transport, uptake, homeostasis, synthesis of antioxidant enzymes, and osmoprotectants. Besides that, microorganisms proved their ability to increase plant tolerance, *Bacillus* spp. represents the dominant bacteria of the rhizosphere zone, characterised as harmless microbes with extraordinary abilities to synthesise many chemical compounds to support plants in confronting salinity stress. In addition, applying arbuscular mycorrhizal fungi (AMF) is a promising method to decrease salinity-induced plant damage as it could enhance the growth rate relative to water content. In addition, there is a demand to search for new salt-tolerant crops with more yield and adaptation to unfavourable environmental conditions. The negative impact of salinity on plant growth and productivity, photosynthesis, stomatal conductance, and changes in plant phytohormones biosynthesis, including abscisic acid and salicylic acid, jasmonic acid, ethylene, cytokinins, gibberellins, and brassinosteroids was discussed in this review. The mechanisms evolved to adapt and/or survive the plants, including ion homeostasis, antioxidants, and osmoprotectants biosynthesis, and the microbial mitigate salt stress. In addition, there are modern approaches to apply innovative methods to modify plants to tolerate salinity, especially in the essential crops producing probable yield with a notable result for further optimisation and investigations.

Keywords: *Bacillus*, ion homeostasis, osmoprotectants, osmotic stress, photosynthesis, ROS scavenging

INTRODUCTION

A significant, sustained debate towards the global agricultural sector includes producing more than 70% of the food supply to feed the world during the world population's growth. Moreover, there is an alarming increase of 2.3–6.0 bln people by 2050 [Conforti (ed.) 2011]. To ensure food security and achieve the minimum level of demand for food, we should be aware that the required rate of increasing the productivity of agriculture is not only the critical approach to overcome the increasing rapidly population year after year but also pay attention to the factors that affect this productivity [Pareek *et al.* 2020]. The other challenge is to produce over 87% of the strategic food crops, especially wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea maize* L.), and others, by 2050 [Kromdijk, Long 2016]. Abiotic stress is one of the leading severe environmental threats that restrict crop productivity, including salinity, water scarcity, heavy metals, and extreme temperatures, which cause an enormous loss in food production [Elsheery, Cao 2008; Elsheery *et al.* 2007; 2008; 2020a, b; Helaly *et al.* 2017; Mantri *et al.* 2012; Nauš 2010]. Among these adverse stresses, soil salinity is one of the significant harsh environmental constraints threatening food security by causing harmful effects, over USD 10 bln of economic losses annually, and limiting the plant growth and productivity depending on the crop. Salts accumulation forms a notable degradation in the soil profile, which causes negatively affects germination, plant vigour, or crop yield, and loses the soil structure in the long term [Flowers 2004; Munns, Tester 2008; Shabala, Cuin 2012; Taha *et al.* 2020]. According to highly cited studies, approximately 45 mln ha (20%) of irrigated lands are saline [FAO 2015; Shelden *et al.* 2016].

Moreover, because food consumption will rise due to higher living standards, food production should increase from 35 to 57% by 2025. This serious debate encourages us to present this review to discuss how to improve agricultural strategies, control this diverse abiotic stress, and achieve a higher crop yield. Such an unfavourable environmental condition has harmful consequences on the global climate changes in long-term exposure through its effects on plants and soil, which are considered the food source of plant health and production [Boyer 1982; Ceccarelli *et al.* 2010].

Land salinisation on a global scale has always been a significant concern for human livelihoods, particularly in the food-producing agricultural industries. According to the most recent estimate, the perennial salinity problem has affected up to 900 mln ha of agricultural land worldwide, causing salinity stress in salt-sensitive crops and lowering productivity and yield [Teo *et al.* 2022). According to the Food and Agriculture Organization, more than 423 mln ha (3%) of topsoil and 833 mln ha (6%) of subsoil are salinised in 118 nations that comprise 85% of the worldwide land area [Lynch *et al.* 2022; UN-Habitat, WHO 2021]. Human-induced salinisation affects over 77 mln acres of land, with Asian regions accounting for 70% of all human-induced salinisation. Furthermore, it is believed that the rate of soil salinisation is growing by up to 10% each year due to several reasons, such as global warming, agricultural management misconduct, and natural processes [Arif *et al.* 2020; Shahid *et al.* 2018].

In addition, several physiological and metabolic changes are involved in the plant-based on the salinity level, duration of exposure, plant health, and growth stage in response to stress conditions [James *et al.* 2011]. Osmotic stress directs cytoplasmic toxicity at high sodium, chloride, and boron – salinity's most common harmful effect on plants. High salinity affects plants by limiting nutrients uptake and assimilation, i.e., K^+ uptake by root cells was disrupted in the saline soil [Elhamahmy *et al.* 2021; Elsheery *et al.* 2020a, b; Hasegawa *et al.* 2000; Naser *et al.* 2016]. Besides, Na^+ stress leads to reduced cell division, cell metabolic changes, and oxidative stress; thus, arable land will be unsuitable for later use and poor-quality irrigation systems [James *et al.* 2011; Shabala, Cuin 2012; Sunkar *et al.* 2007]. Recent studies [Etesami, Noori 2019; Kumar *et al.* 2021; Shrivastava, Kumar 2015] observed a significant reduction in rice plants' growth and productivity under soil salinity in root length, number of tillers, and grain yield. All the rice varieties had been negatively affected by the high salt levels. The tallest plants were 58.5 cm, while the shortest were 45.0 cm at the highest salt level (60 $mmol \cdot dm^{-3}$ NaCl). Salt stress affected more than 20% of cultivated land worldwide [Hasanuzzaman *et al.* 2013] by producing Na^+ and Cl^-, which caused many physiological disorders in plants due to increased salt levels daily. Therefore, it is necessary to reduce these unfavourable effects. This is a massive concern for many global researchers to cope with the required food security and agricultural productivity rate. Since plants cannot control this abiotic stress, they have evolved several mechanisms to adapt and/or survive under high salt concentration soils through two strategies: stress tolerance (tolerating its presence within the cells) or stress avoidance (excluding salt from their cells). Furthermore, improving plant stress tolerance is critical for plant productivity and food sustainability to enhance water and fertiliser efficiency under environmental stress conditions [Zhu 2016]. Thus, the review highlights the harmful impact of salt on the plant, how plants respond to salt stress, and the role of different biochemical attributes and critical antioxidants in withstanding salt stress.

SALT STRESS INDUCES CHALLENGING IMPACTS ON PLANT GROWTH AND PRODUCTIVITY

Salinity negatively influences both leaf expansion and water levels. In addition, the imbalance in the plant water status, turgor reduction, and stomatal closure, thus causing growth inhibition through the reduction in photosynthesis. Interestingly, plant response by osmotic adjustment often involves raising Na^+ and Cl^- contents in different plant tissues. Excess inorganic ions can have significant toxic consequences and cause cell death. The osmotic adjustment reduced the fresh and dry weight ratio, increased apoplastic water content, and directly compatible solute aggregation [Elhamahmy *et al.* 2021; Elsheery *et al.* 2020a, b; Hernández, Almansa 2002; Naser *et al.* 2016]. The seed germination of broccoli and cauliflower was grown under salt-stress conditions; the salt-treated plants showed changes in the seed physiological activity. In addition, water levels, amino acid content, and nutrient reservation in the germinated seeds are impacted under saline stress [Arif *et al.* 2020; Wu *et al.* 2019]. In addition, several plant species significantly reduced growth parameters under salt stress (e.g., reduction in phosphate activity in *Arabidopsis*) [Nasri *et al.* 2016]. In addition, the leaf and root dry weight and waterleaf levels were reduced in *Balanites aegyptiacea* [Khamis *et al.* 2016]. Reductions in the numbers and weight of cotton balls and the crop quality were observed when plants were grown under salt conditions [Wang *et al.* 2018].

Moreover, salinity stress reduced tomato (*Solanum Lycopersicum* L.) growth parameters and leaf water potential [Xue *et al.* 2021], similar to the pea (*Pisum sativum* L.) salt-treated plant [Hernández, Almansa 2002]. Salinity affects the plant growth parameters of different strawberry cultivars grown under irrigation with 35 mM NaCl. The shoot and dry root weight and relative leaf water levels were reduced after seven days by 29–33%, 45–15%, and 11–13%, respectively [Karlidag *et al.* 2011]. Interestingly, there was a variation in soil salinity among the genotypes of the same plant species. For instance, three different genotypes of *Populus alba*: 6K3 (sensitive), 2AS11 (moderately tolerant), and 14P11 (tolerant), were grown under different levels of salt stress (i.e., 50–250 mM NaCl). After ten days, there was a significant genotypic variation in growth parameters. For example, the 14P11 genotype significantly reduced leaf length and the lowest abscission rate. Moreover, genotype 14P11 significantly revealed the smaller epidermal cells and the highest stomatal density values. Different modulation amongst the salt-treated plants was reported in stomata expansion compared to the epidermal cells. In contrast, the 6K3 genotype revealed several features, such as leaf necrosis and the highest abscission rate. However, 2AS11, as a tolerant genotype, showed the lowest leaf physiology and morphology [Abbruzzese *et al.* 2009].

CHANGES IN PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE OF PLANTS GROWN UNDER SALINITY

Increasing plant growth and development is the consequence of physiological processes that are interconnected and controlled. Various external conditions impact physiological processes, which define how plants respond to abiotic stress. For example, environmental factors that limit plant development cannot be attributed to a simple physiological mechanism. Photosynthesis which increases the plant biomass, is considered the most important physiological mechanism. Therefore, the environmental factors that constrain photosynthesis negatively affect plant growth.

Furthermore, salinity can cause short or long-term impacts on the photosynthesis mechanism. For example, after several hours or one to two days of starting the treatment, carbon absorption is significantly reduced as a short-term impact. After several days of the treatment, the salt accumulates in grown leaves, causing a decline in carbon absorption and a reduction in net photosynthetic rate as a long-term impact [Parida, Das 2005]. In addition, several studies stated that salt stress decreases photosynthesis efficiency. For instance, Khavari-Nejad and Chaparzadeh [1998] reported the rate of photosynthesis and chlorophyll content, besides the respiration and assimilation of CO_2 in alfalfa (*Medicago sativa* L.) leaves, decreased under salt stress. In addition, increasing salt concentration in four rice lines (*Oryza sativa* L.) decreased the emission of the chlorophyll fluorescence and the activities of PSI (photosystem I) and PSII (photosystem II), which caused a significant decline in the net photosynthetic efficiency [Tiwari *et al.* 1998]. Finally, Moradi and Ismail [2007] observed that salt stress gradually decreased the stomatal closure, CO_2 fixation, and electron transport in the IR29 sensitive cultivar compared to IR651 as the tolerant cultivar. Several mechanisms are involved in the photosynthesis process, such as enzymes and intermediate products. Finally, the efficiency of photosynthesis is affected through several metabolic paths, for instance, the photosynthetic elements that transport across intracellular pathways, the photochemical reactions, the carbon absorption enzymes, and the components of the photosynthetic apparatus [Parida, Das 2005].

Besides reducing photochemical efficiency, the stomatal and mesophyll conductance was reduced in different salt-treated genotypes of olive (*Olea europea* L.) irrigated with saline water at 200 mM [Loreto *et al.* 2003]. The photosynthetic rate was reduced in the rice salt-treated plant, as well as the osmotic potential, rate of electron transport, and CO_2 assimilation in rice leaf chloroplasts. However, the photosynthetic rate was decreased because of the leaf chloroplasts. In addition, salinity was reduced to the osmotic potential of the leaves because of stomatal limitations. The reduction in the mesophyll conductance of salt-stressed plant leaves was connected to the ion and osmotic levels [Wang *et al.* 2018a, b]. However, stomatal conductance constraints reduce photosynthetic activity, reducing CO_2 availability in the carboxylation mechanism.

Interestingly, the first stage of the negative impact of salinity on photosynthesis of barley (*Hordeum vulgare*) cultivars is attributed to the limitation of stomatal conductance more than the decline in PSII activity [Kalaji *et al.* 2011]. The effects of salinity on the stomatal conductance were reported through two cultivars of strawberries grown under irrigation with 35 mM NaCl. After seven days, the stomata conductance and leaf chlorophyll reading values were reduced under salt stress to 71–55% and 12–13%, respectively [Karlidag *et al.* 2011]. In addition, several parameters related to stomata closure were negatively affected in tomatoes grown under different salt concentrations. In addition, salinity has promoted the reduction in several stomatal factors (length, width, perimeter, area, and density), resulting in a reduction in photosynthetic and transpiration rate and chlorophyll content [Xue *et al.* 2021]. Furthermore, in the pea salt-treated plant, the stomata conductance was reduced after 48 h of salt treatment compared to the control [Hernández, Almansa 2002].

SALT STRESS-INDUCED CHANGES IN PLANT PHYTOHORMONES

Osmolytes and plant hormones are established to play critical roles in harsh environments, for instance, Auxin (IAA), Cytokinins (CKs), abscisic acid (ABA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), brassinosteroids (BRs), Jasmonic acid (JAs), and Strigolactone (SL). Several plant phytohormones are up-regulated in response to increasing salt concentration in the soil, such as abscisic acid, cytokinin, and jasmonates [Elhamahmy *et al.* 2021; Elsheery *et al.* 2020a, b; Naser *et al.* 2016; Parida, Das 2005] (Fig. 1).

Abscisic acid (ABA) is a tiny molecule that plays a crucial role in the abscission of plant leaves. It is considered a “stress hormone” due to its responsiveness and specific involvement in plant adaptation to abiotic stressors [Müller 2021; Obroucheva 2021]. It is present in plant roots and terminal buds near the top of the plant. ABA biosynthesis occurs in two places, starting in the plastids and ending in the cytosol. Numerous studies showed that the salt-treated plant contains a significant increment in ABA levels. For instance, [Jia *et al.* 2002] reported that the accumula-

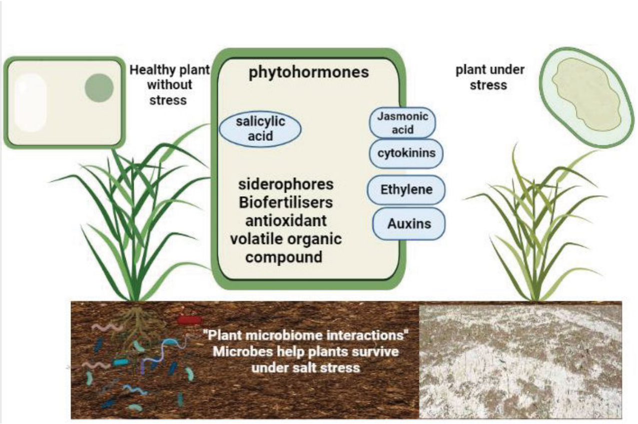

Fig. 1. Salt stress impact on plant biology, growth and yield reduction, plant's response to abiotic stress under the influence of phytohormones and growth promoters; source: own study

tion of ABA in roots under salt stress increased significantly up to 10-fold compared to about 1-fold in shoots. In facultatively halophytic *Lophopyrum elongatum* and the low salt-tolerant wheat, salt tolerance is increased when plants adapt to salt conditions rather than being shocked progressively. ABA regulates the acclimatisation process, where the pre-treatment with ABA enhances salt shock resistance. The ABA-induced adaptation is quick and associated with the upregulation of the root's early salt-related genes. The tolerance of salt shock is better in *L. elongatum* than in wheat, and the tolerance is regulated by chromosome 3E in the *L. elongatum* genome and chromosomes 3A and 3D in wheat. Thus, the salt shock response through ABA in both species is connected to chromosome 3 [Elsheery *et al.* 2020a, b; Naser *et al.* 2016; Noaman *et al.* 2002].

Interestingly the increase of ABA in the salt-treated plant enhances several changes at the plant's physiological levels to cope with salinity. Such as, in *Mesembryanthemum crystallinum*, the level of ABA was increased to 8- to 10-fold under salt stress enabling the switching from C3 to crassulacean acid metabolism (CAM) and proline production in this plant [Thomas *et al.* 1992]. Moreover, by rapidly changing guard cell ion fluxes, ABA enhances the stomatal conductance in plants under salt stress. Another ABA feature involves changes in the expression of ABA-related genes. Studies of ABA-responsive promoters have shown a wide range of possible cis-acting regulatory elements. In addition, several downstream signalling elements exhibited a significant role in ABA signal transduction, such as reversible protein phosphorylation, changes in cytosolic calcium levels, and pH [Parida, Das 2005]. Nevertheless, during salinity, the level of the ABA was increased due to the increased Ca^{2+} uptake, which helps the membrane integrity maintenance and allows the plant to control the nutrients' transport and uptake under long-term salt stress [Chen *et al.* 2001].

Salicylic acid (SA) is a natural phenolic molecule that modulates pathogenesis-related protein expression. Plant growth, ripening, development, and abiotic stress responses and defense responses are regulated mainly by it [Miura, Tada 2014; Rivas-San Vicente, Plasencia 2011]. In plants' regular aerobic metabolism, several reactive oxygen species (ROS), such as (•) OH, (•) $O_2(-)$, and H_2O_2, are formed and scavenged. However, with deficient levels of ROS, significant signal transduction activities and triggering and/or directing plant responses to a range of stress conditions can all be done. However, oxidative stress occurs when (abiotic) stressors disrupt the balance between generating and scavenging ROS. In addition, various impacts, such as oxidative modification of vital macromolecules, cell death, and plant growth and development, can occur under uncontrolled oxidative stress [Gill, Tuteja 2010]. Through interactions with various signalling pathways, including SA-mediated signalling pathways, apoplastic-ROS have been identified as cell death regulators [Overmyer *et al.* 2003]. SA-dependent and independent signalling components and ROS-signalling resulted in an appropriate defence response. SA can activate a protein kinase and serve as a signal for the development of systemic acquired resistance. The function of the NPR1 protein in SA communication under biotic and abiotic stress is showed in (Fig. 2). In addition, the SA receptor NPR1 (non-expresser of PR (pathogenesis-related) protein 1) regulates PR gene expression in an SA-dependent way [Morinaka *et al.* 2006]. SA also binds to NPR1 and NPR4 (prologues of NPR1). Finally, an oligomeric NPR1 in an oxidised state can be detected in the cytoplasm with low SA concentrations. SA accumulates in the cellular redox state when stress levels grow, activating NPR1 monomers while lowering oxidised NPR1 oligomers. SA-NPR3/NPR4 interaction causes oligomeric NPR1 to become monomeric NPR1, which goes into the nucleus and interacts with specific transcription activators, co-activating the SA-responsive PR gene [Fu *et al.* 2012].

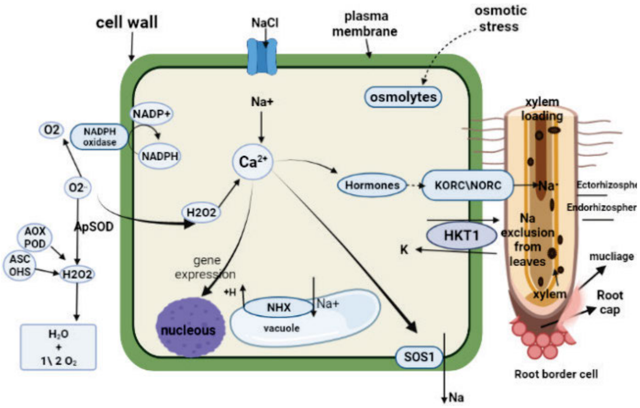

Fig. 2. The synergistic effects of salinity stress on cell membranes and their mechanistic response through cellular influx, sensing, and signalling; source: own study

Jasmonic acid is another phytohormone used throughout the plant arsenal to cope with soil salinity. Besides improving plant tolerance to salinity, jasmonic acid exhibited significant roles in plant growth, floral development, fruit ripening, and protecting the plant from pathogen infection, insect attack, and wounding [Song *et al.* 2021]. Jasmonates are considered critical signalling molecules in the plant defence mechanism. The jasmonate signalling components, such as jasmonate ZIM-domain (JAZ) and MYC2, have been recognised as critical factors in the interaction of jasmonic acid with another hormone signalling pathway. However, the orchestration coordination between jasmonate and the other phytohormones in the signal transduction pathway remains elusive [Delgado *et al.* 2021]. Under salt stress, endogenous levels of JA increased in rice roots, which was reported to mitigate the adverse effects of salinity stress. In addition, plant antioxidant machinery can be activated with JAs to alleviate heavy metal stress. In addition, MeJA accumulates phytochelatins in *A. thaliana* plants, providing Cu and Cd stress [Maksymiec *et al.* 2007; Yan *et al.* 2013]. In addition, pre-treatment wheat and rice with jasmonate improved their salt tolerance and significantly reduced the Na^+ ion content in both plants [Ghorbani Javid *et al.* 2011; Qiu *et al.* 2014]. Additionally, it promotes the recovery process through seedling development and photosynthetic activity of soybean after salt stress conditions [Yoon *et al.* 2009].

Ethylene (ET) is a gaseous phytohormone that regulates plant stress responses. In addition, it plays a role in fruit ripening, floral senescence, and leaf and petal abscission. S-adenosyl-L-methionine (AdoMet) and the cyclic non-protein amino acid ACC biosynthesise it from methionine. The conversion of AdoMet to ACC is catalysed by ACC synthase, while the conversion of ACC to ethylene is catalysed by ACC oxidase. Plant endogenous ET levels are affected by abiotic stressors such as low temperature and salinity. Higher ET concentrations improved tolerance [Groen, Whiteman 2014]. For heat stress adaptation, ET is also required for plants [Larkindale *et al.* 2005]. Environmental stress promotes ET levels, improving the probability of plants surviving under these extreme conditions. ET is intended to function by controlling gene expression, one of the ethylene signal's effectors. ET synergises when combined with other phytohormones like JA and SA. These are the most critical players in plants' pest and disease defence regulation. ET and ABA appear to have a synergistic or antagonistic effect on plant growth and development, according to [Kazan 2013; Yin *et al.* 2015].

Cytokinins are another phytohormones in the plant's arsenal to cope with soil salinity. They are considered a significant factor in plant development and growth and regulate plant response to salinity stress; there are several naturally abundant isoprenoid cytokinins such as N6-isopentenyl adenine (IP), trans-zeatin (tZ), and cis-zeatin. The salt tolerance in (*Medicago sativa* L.) was improved through the overexpression of the cytokinin gene (CKXs) in the roots [Li *et al.* 2019]. Moreover, the ability of *Arabidopsis* to cope with the soil salinity was increased via the induction of cytokinin production through the up-regulation of cytokinin biosynthetic gene AtIPT8 (adenosine phosphate – isopentenyl transferase 8), which increased the induction of enzymatic antioxidants resulting in increasing the activity of ROS that finally improved the salinity stress tolerance in *Arabidopsis* [Wang *et al.* 2015]. Moreover, the total soluble sugars and the yield of rice were increased under salt treatment through the application of exogenous phytohormones such as Auxin (indole-3-acetic acid IAA) and kinetin (KIN) [Gujjar *et al.* 2021].

In plants, gibberellins are other plant phytohormones that can also enhance sugar signalling, osmolyte synthesis, and antioxidant activity, which benefits in scavenging reactive oxygen species and sustaining cell osmotic adjustment during soil salinity conditions. Moreover, it contributes to maintaining plant water levels and photosynthesis efficiency to mitigate the adverse effects of soil salinity and improve plant salt tolerance [Chele *et al.* 2021]. In addition, polyamines accumulate in massive amounts in plant cells during salinity, regulating vital processes such as development, growth, and proliferation and acting as an osmoprotectant, retaining cell osmotic potential [Choudhary *et al.* 2022].

Brassinosteroids (BRs) are new polyhydroxy steroidal plant hormones that help plants grow and develop rapidly. They were discovered and identified in the pollen of the rape plant (*Brassica napus*). Plants have been found to have over 70 different BRs. The three most bioactive BRs, brassinolide, 28-homobrassinolide, and 24-epibrassinolide, are extensively employed in physiological and experimental studies [Tong, Chu 2018]. In addition, they participate in various developmental stages, including stem and root growth, floral initiation, and flower and fruit development. In addition, they are involved in several developmental processes, such as stem and root growth, floral initiation, and flower and fruit development [Bajguz, Hayat 2009].

SALT TOLERANCE STRATEGIES

Efficient strategies to boost plant salt tolerance are indispensable for understanding several plants' responses under salt stress, such as physiological and molecular mechanisms [Chen *et al.* 2021; Wang *et al.* 2021]. Therefore, it will be essential to cultivate and discover new salt-tolerant crops. Abiotic stress resistance is a comparative approach because of variations in salt tolerance between the plant species and varieties. For instance, some staple crops, i.e., barley (*Hordeum vulgare*), are more salt-tolerant than wheat and rice [Cui *et al.* 2021; Zhang *et al.* 2022]. Since different crops are more drought-resistant than rice [Niu *et al.* 2022], plant biologists seek to identify the different mechanisms, set of genes, and expression level that helps plants survive under stressful conditions, improving the yield of salt-tolerant species [Hossain, Islam 2022; Kumar *et al.* 2022; Mishra *et al.* 2021]. Attention to that aspect, we will present some fundamental mechanisms to improve plants' tolerance responses under salt conditions. Finally, an intriguing question regarding salt tolerance needs to be explained: "How do plants sense and adapt to soil salinisation with their various morphological, physiological, biochemical, and genetic expression responses?" In addition, it would help regulate plant adaptation, enhance salinity-tolerant crops, and increase food production. In addition, plants were divided into glycophytes (salt-sensitive group) and halophytes (salt tolerance group). The primary response of plants as individual and/or synergistic cells, either salt tolerance or sensitivity, is affected by several physiological and metabolic changes to survive in a saline environment. Finally, salt stress affects plant growth [Noor *et al.* 2022; Tran *et al.* 2021]. Salt tolerance has different physiological and biochemical mechanisms, including ion transport and uptake, ion homeostasis, a synthetic antioxidant enzyme, regulation hormones, andbiosynthetic osmoprotectants..

a) Ion homeostasis

Homeostasis is defined as the predisposition of a cell to sustain its response to any conflict, environmental stress, or excites function activity towards these unfavourable conditions. Plant response to salt tolerance with different species evolved a specific mechanism to adapt to the saline environment, such as salt glands excreting excess salts in a few plant species. Ion transport and solubilisation are crucial in plant growth and play an essential role under salt stress during the life journey. It is known that ion transport processes across the tonoplast and the plasma membrane are essential for controlling sodium uptake and vacuole of the plant compartmentation, which pumps it into and out of the vacuole. Thus, plants exposed to salt stress reduce the water potential and accumulate in the cytosol by adjusting the osmotic imbalance and accumulating ions from the external environment.

A highly cited study mentioned that Na^+ transport might occur through outward rectifying cation channels. Excessive exposure to salt stress and plasma membrane depolarisation increases the possibility of outward rectifying cation channels in wheat root and tobacco cells, allowing the sodium influx to occur in its steep electrochemical gradient. Hence, physiological or biochemical strategies for salt tolerance that help reduce the open probability of these outward-rectifying channels would decrease pass Na+ into the cell as one of the adaptive processes in the saline environment to avoid plant growth and cell division [Chen *et al.* 2007; Schachtman *et al.* 1991].

Presumably, maintaining the ion homeostasis for both K^+ and Na^+ is crucial because regulating ion uptake provides a clear understanding of the ion homeostasis ion in plant cells. Besides, the explanation of plants' possibility to adapt and/or survive in excessive salt accumulation improves the agricultural efficiency in the soil salinity with large-scale crops globally. For example, plant cells can sense the sodium-specific signals of slat stress, which is probably essential in the regulation of Na^+ transport and the transcription of AtNHX1, the gene encoding the vacuolar Na^+/H^+ exchanger under osmotic stress. Genetic evidence to explain these signals' vital roles is still lacking, but supposedly, Na^+ ions can be sensed by plants either before or after entering the cells [Yokoi *et al.* 2002]. For instance, sodium transport affects the apoplastic pathway and silica deposition in the cell wall [Yeo *et al.* 1999]. Studies by Dietz *et al.* [2001] and Wang *et al.* [2001] suggested that the Na^+ ion transports to the vacuole via Na^+/H^+ antiporter after entering the cells. They mentioned two types of H^+ pumps in the vacuole's cytoplasmic membrane: vacuolar pyrophosphatase (V-PPase) and vacuolar-type H^+-ATPase (V-ATPase). The last one is the most dominant H^+ pump in the plant cell. The experimental work by Oliviera Otoch *et al.* [2001] revealed that vacuolar-type H^+-ATPase pumps increased during salt exposure with inhibition of activity V-PPase, proving the importance of genetic regulation under stressful conditions. This part of the review presents a logical sequence for the underlying mechanism of stress signals (Fig. 2). Little is known about the mechanism of Na^+ sensing in the cellular system. Numerous studies have investigated a salt overly sensitive (SOS) stress signalling pathway and elucidated its role in salt tolerance and ion uptake. The SOS system consists of three proteins, SOS1, SOS2, and SOS3. SOS1 protein encodes a plasma membrane Na^+/H^+ antiporter with more than 700 amino acids in the cytoplasm. It plays an essential role in Na^+ efflux regulation at the cellular level; Na^+ transports from root to shoot and reduces salt stress by regulating the gene expression of this protein [Shi, Zhu 2002]. This exchanger activity is necessary for Na^+ efflux in *Arabidopsis* plants; thus, the function of the SOS1 protein is a transporter. A sensor of Na^+ and its activity is detected in the salt-stressed plant but not in the unstressed plant [Hussain *et al.* 2021]. Like SNF1 protein in yeast and AMP-activated kinase (AMPK) in animals, the second protein is the SOS2 gene consisting of an N-terminal catalytic domain and a unique carboxy-terminal regulatory domain [Gupta *et al.* 2021; Liu *et al.* 2000]. In addition, it encodes a serine/threonine kinase under salt stress. Finally, the C-terminal regulatory domain of SOS2 protein contains 21 amino acid long sequences called a NAF domain.

The third one is SOS3; this protein has an essential role in configuring the signalling pathways for salt stress tolerance through the myristoylation Ca^+ binding protein site, which senses the cytosolic calcium signal of salt stress [Zhang *et al.* 2022]. It also activates the kinase enzyme by interacting with SOS2 and SOS3 proteins. Besides conferring this stress, it regulates pH homeostasis and vacuole functions [Martínez-Atienza *et al.* 2006; Oh *et al.* 2010].

SOS3 has a significant sequence in yeast and animals with calcineurin B subunit and neuronal calcium sensors [Liu, Zhu 1998]. The SOS1 gene is upregulated under salt stress on the transcription level, and this posttranscriptional regulation appears partly interact with both SOS2 and SOS3 [Zhu 2003]. Interestingly, there is a positive relationship between the high-level concentration of Na^+ and intracellular Ca^+, which induces its binding with the SOS3 protein to confer salt tolerance. SOS1 consists of a long C-terminal tail (~700 amino acids); this domain is a target site for SOS2 phosphorylation in the activation loop of kinase and phosphorylated SOS1 during the interaction complex between SOS2 and SOS3 on the plasma membrane, resulting in increasing the Na^+ efflux, reducing the toxicity of Na^+ as well [Martínez-Atienza *et al.* 2006].

Regulation and/or controlling the ion concentration for plant uptake under stress conditions is a process plants can develop to efficiently regulate the ion concentrations at a low level in the cytoplasm. This unbalanced concentration during a high level of Na under salt environments inhabits the K uptake by the plant, competes with Na^+, disrupts K^+ transport, and decreases its solubility in the soil. The ion transport process is controlled by several factors, i.e., the channel or carrier proteins, and the receptor types during the saline condition [Deinlein *et al.* 2014]. The findings concluded that the sense of extracellular Na^+ might be through receptors, while the control of intracellular Na^+ sensing is by membrane proteins or specific enzymes in the cytoplasm. Understanding the underlying mechanisms and evolution of plant stress response could provide new aspects for improving crops' efficiency under abiotic stress.

b) Antioxidant machinery and osmoprotectants biosynthesis

Abiotic stressors (e.g., salt, drought, pesticides, and heat) negatively influence plants' physiological and biochemical processes, including hormone signalling and antioxidant systems [Sharma *et al.* 2016]. Salinity stress induces free radical formation, i.e., hydroxyl radical (OH^-), superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and singlet oxygen. ROS factors could lead to increased oxidative stress in the cellular system in response to salt stress. For example, they might disrupt vital cellular processes, i.e., protein, DNA, and gene expression, protecting the cell from apoptosis in continuous stress exposure [Elsheery *et al.* 2020a, b; Gupta *et al.* 2005; Naser *et al.* 2016]. Plants adapt to avoid risk and boost their ability to live in harsh conditions through accumulating osmolytes and other appropriate solutes to protect their cellular machinery from various environmental stressors (Fig. 1). Glycine betaine (GB), sugars (mannitol, sorbitol, trehalose), polyamines, and proline are essential factors to help plants under stresses.

Abiotic stress induces host plants to produce some sugars, e.g., trehalose, mannitol, and galactinol, to accumulate in plants. Numerous genes produce these organic solutes, which help transgenic plants generate abiotic stress resistance [Taji *et al.* 2002]. In addition, plant phytohormones have a role in various biochemical and physiological processes. However, plant tolerance in challenging environments depends on reducing abiotic stress [Shahzad *et al.* 2018; Tanveer *et al.* 2019].

Enormous studies show that the function of compatible solutes such as proline, sugars, polyols, and glycine betaine is synthesised and induced in various amounts within plant species during stressful conditions. These organic compounds' primary role is to protect the cell's structure via stress exposure and maintain the osmotic balance. Besides, some amino acids are decreased in the stress environment, i.e., cysteine, methionine, and arginine, which are considered the genetic code's backbone during the central dogma of life. Although, proline level will be raised in salinity stress response and accumulated as an indicator of high-level salt stress. This compound's synthetic pathways are regulated by two enzymes, pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase [Ashraf, Foolad 2007; Chen *et al.* 2007; Elsheery *et al.* 2020a, b; Naser *et al.* 2016].

Another study on olive (*Olea europaea* L.) reported that proline supplemented increased plant growth and antioxidant enzymes, enhancing salt tolerance and photosynthetic activity [Ben Ahmed *et al.* 2010]. Various studies revealed a positive relationship between plant salt tolerance and proline increase [Martinez *et al.* 1996; Surekha *et al.* 2014]. A recent study by Kibria *et al.* [2017] evaluated the proline content in saline conditions with salt-tolerant rice genotypes, which increased with high salt levels. They also mentioned that proline content decreased at 60 mmol·dm^{-3} NaCl with the salt-sensitive genotype, while the salt-tolerant rice genotype accumulated approximately 2.2-fold higher proline than the control. Reducing proline accumulation in the salt-sensitive rice genotype might be a primary reason for high degradation and low proline synthesis in a saline environment. Another critical role by some sugars, i.e., glucose, sucrose, fructose, and trehalose accumulation, have a physiological response by an osmoprotective function during salt stress. For instance, sucrose content was increased in tomato plants in response to a salinity environment based on phosphate synthase enzyme. However, it was observed that sugar content has decreased in different rice genotypes, and starch content decreased in rice roots while unaffected in the shoot [Parida *et al.* 2004].

Glycine betaine (GB) is a nontoxic compatible solute that helps the plant cell under abiotic stress, i.e., salt. It has a crucial role in stress mitigation which protects the cellular systems by reducing stress damage and osmotic adjustment [Mbarki *et al.* 2018]. It appears to be the most influential member of widely ranging protective solutes under stress conditions in which the biosynthesis of GB increases the abiotic stress tolerance in crops. Moreover, GB's accumulation increased the crop yield under normal conditions and correlated with enhancing tolerance for various stressful conditions [Chen, Murata 2008]. Foliar spray pre-treatment with glycine betaine has a positive effect on rice seedlings in saline conditions (150 mM NaCl) and protects these plants from structural damage, i.e., the disintegration of grana cells and mitochondria disruption, as well as increases both photosynthetic and growth rates [Rahman *et al.* 2002]. This function pathway consists of N-methylation, which catalyses into glycine sarcosine N-methyl transferase (GSMT) and sarcosine dimethylglycine N-methyl transferase (SDMT) [Ahmad *et al.* 2013]. The application of glycine betaine has been studied extensively in diverse strategic crops with different types of abiotic stress, i.e., *Arabidopsis thaliana*, *Oryza sativa*, *Hordeum vulgare*, *Zea mays*, and *Triticum aestivum* under drought and salt stress [Landi *et al.* 2017]. Thus, the foliar spray of GB at the reproductive stage or the early stages of plant growth enhanced stress tolerance by induction of specific genes related to stress tolerance and increased the numbers of reproductive organs, i.e., flowers, plant developmental patterns, and the yield [Chen, Murata 2008].

On the other hand, oxygen is an abundant vital element for all living organisms' sustainability; one of the water components by reducing O_2 to H_2O is one of the most critical necessities on Earth. However, incomplete reduction of O_2 would lead to the generation of highly active ROS, causing oxidation by producing various oxidative radicals. In addition, antioxidant enzymes' role in keeping the ROS signals at low levels and reducing their damage affects the cellular molecules [Apel, Hirt 2004]. In addition, a positive association has been shown to increase the antioxidant activities of plant salt stress response and decrease oxidative damage, improving salt tolerance. In addition, antioxidant metabolites, including different enzymes that provide a pivotal role in salinity tolerance by reactive oxygen species (ROS) detoxification, protect the plant cells from the negative impact of salt stress (Fig. 3).

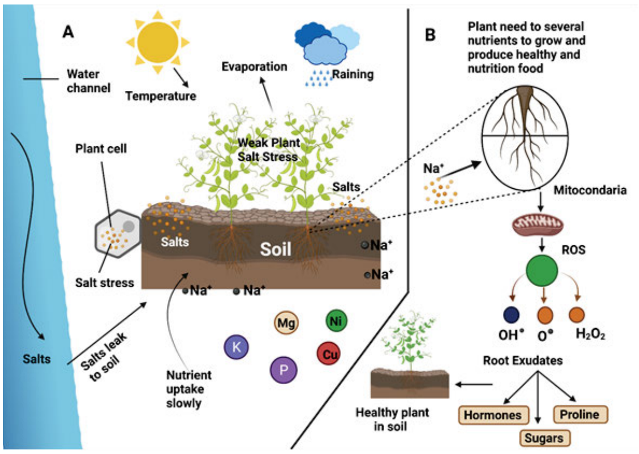

Fig. 3. Plant response to various abiotic stresses and using osmolytes to counteract reactive oxygen species (ROS) under stressful conditions; source: own study

c) *Bacillus* endophytes mitigate salt stress

Plant growth-promoting bacteria (PGPB) play an essential role in the biological function of the rhizosphere, which improves agricultural crop yield and health [Orozco-Mosqueda *et al.* 2020; 2021]. Bacteria live in the rhizosphere's soil zone by consuming plant root exudates [Li *et al.* 2021]. They include free-living soil and symbiotic bacteria [White *et al.* 2018]. Abiotic stress tolerance, seed germination, shoot, root weights, root development, yield, phosphate, and nitrogen uptake is improved by bacterial endophytes. However, the ability of PGPB to improve crop production is influenced by several direct and indirect mechanisms, including inorganic phosphate and other mineral solubilisation, increased nutrient intake, nitrogen fixation, and plant hormone production [Martínez-Viveros *et al.* 2010]. Moreover, PGPB protects the plants from severe abiotic factors, i.e., drought and temperature stress [Sarma, Saikia 2014], salinity stress [Bensidhoum, Nabti 2019; Sandrini *et al.* 2022], heavy metal stress, and chilling plant injury [Singh *et al.* 2018]. PGPB could mitigate the salt stress through various mechanisms studies in some plants, as shown in Table 1. The initial effect of the salinity issue is osmotic stress, which causes a change in the water balance. It leads to stomatal closure [Mukhopadhyay *et al.* 2021], loss in the leaf areagas exchange imbalance, and loss of leaf area. This impacts plant growth; carbohydrates accumulate, especially in meristems, affecting new tissue formation [Ilangumaran, Smith 2017]. Soil rhizosphere is rich with PGPB bacteria producing exopolysaccharides, high-molecular-weight organic polymers [Etesami, Adl 2020], which play essential roles in defence against environmental stress [Gupta, Diwan 2017]. In addition, exopolysaccharides improve soil aeration and porosity by increasing soil particle adhesion to bacteria resulting in macropore formation. These soil particles attaching and the structure increasing will reduce the initial osmotic stress [Shrivastava, Kumar 2015]. Exopolysacch arides also chelate sodium ions in the rhizosphere, making them more conducive to plant root proliferation [Arora *et al.* 2012]. The other essential mechanism involved phytohormones production; bacteria could release exogenous phytohormones to increase the plant salt tolerance as indole acetic acid (IAA) and abscisic acid (ABA), especially IAA, which produce 80% of rhizospheric bacteria [Ali *et al.* 2022; Zakharova *et al.* 1999]. Indole-3-acetic acid regulates cell division, plant growth, root elongation, and leaf differentiation [Wu *et al.* 2021]. Abscisic acid acts as a cellular signal which regulates seed germination and induces different genes in response to drought and saline conditions [Jovanović, Radović 2021]. Bacteria-producing Auxin stimulates cell division, seed germination, tissue differentiation, and root elongation [Méndez-Gómez *et al.* 2021; Singh *et al.* 2021]. Indole acetic acid (IAA) was decreased in plants under salt stress; however, it increased after inoculation with bacteria on the cotton rhizosphere [Egamberdieva *et al.* 2015]. Abscisic acid (ABA) and IAA levels were observed in wheat plants after inoculation with *Bacillus cereus* [Numan *et al.* 2018]. The overproduction of IAA improves plant salt stress tolerance by increasing proline levels as well as other phytohormones such as cytokinin (CK) and abscisic acid (ABA) [Neshat *et al.* 2022] (Fig. 4).

Table 1. Promotion of different plants under salinity stress with *Bacillus* sp.

Bacterial strains	Effects on plant	Plant species	References
Bacillus spp.	under salt, stress promotes plant development through phosphate solubilisation and siderophore synthesis	*Zea mays* L.	Ullah and Bano [2015]
	plant biomass, carbohydrates, water homeostasis, and soil aggregate have improved		Vardharajula *et al.* [2011]
Bacillus megaterium	root tolerance increased, and the aquaporin genes were upregulated		Marulanda *et al.* [2010]
Bacillus amyloliquefaciens SN13	plant biomass, the water content increase, while proline and ROS decreases	*Oryza sativa* L.	Chauhan *et al.* [2019]
Bacillus amyloliquefaciens NBRISN13	modify rhizosphere microbial community		Nautiyal *et al.* [2013]
Bacillus pumilus	plant biomass increases while lipid peroxidation and sod activity decreases		Mohan and Gupta [2015]
Bacillus pumilis	plant biomass increases by the accumulation of glycine betaine-like compounds		Jha *et al.* [2011]
Bacillus aquimaris	plant biomass, soluble sugars, and proline increase	*Triticum aestivum* L.	Upadhyay and Singh [2015]
Bacillus pumilus	plant antioxidants increase		Khan *et al.* [2016]
Bacillus pumilus	lipid peroxidation and SOD activity decreases		Jha and Subramanian [2014]
Bacillus pumilus FAB10	plant biomass increases		Ansari *et al.* [2019]
Bacillus megaterium, B. tequilensis	plant biomass, soluble sugars, and proline increase		Haroon *et al.* [2021]
Bacillus subtilis SU47	plant biomass, soluble sugars, and proline increase		Upadhyay *et al.* [2012]
Bacillus subtilis	plant biomass and nutrient uptake increase		Talebi Atouei *et al.* [2019]
Bacillus spp.	plant growth promotion, root proliferation, increased proline content, and antioxidant activities, and decreased ethylene in the plant	*Capsicum annuum* L.	Wang *et al.* [2018]
Bacillus spp.	plant proline increases		Sziderics *et al.* [2007]
Bacillus amyloliquefaciens HM6	promote plant growth, root architecture under water stress	*Hordeum vulgare* L.	Kasim *et al.* [2016]
Bacillus spp.	plant biomass, photosynthesis, and water content increase	*Glycine max* L.	Kumari *et al.* [2015]
Bacillus japonicum, B. thuringiensis NEB17	PEP carboxylase and antioxidant glutathione-S-transferase up-regulation		Subramanian *et al.* [2016]

cont. Tab. 1

Bacterial strains	Effects on plant	Plant species	References
Bacillus megaterium	upregulation of jasmonic acid metabolism	*Arabidopsis thaliana* L.	Erice *et al.* [2017]
Bacillus amyloliquefaciens FZB42	plant biomass and nutrient uptake increase	*Arabidopsis thaliana* L.	Liu *et al.* [2017]
Bacillus licheniformis, B. subtilis, Bacillus spp.	plant biomass increases	*Fragaria* x *ananassa*	Seema *et al.* [2018]
Bacillus subtilis	plant biomass and nutrient uptake increase	*Puccinellia tenuiflora* Scribn., Merr.	Niu *et al.* [2016]

Source: own elaboration.

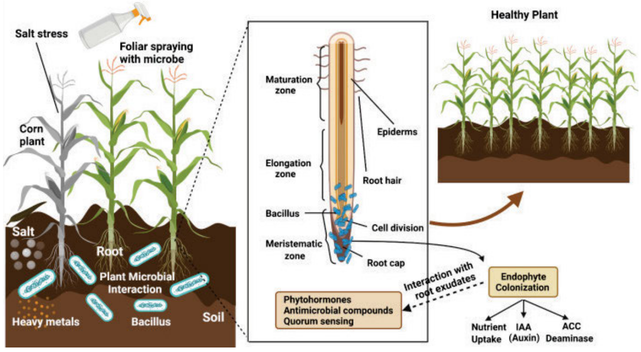

Fig. 4. Plant-growth-promoting microbes take action to help the host plants respond to environmental stress; source: own study

Bacillus spp. represents the dominant bacteria of the rhizosphere zone, characterised as harmless microbes with extraordinary abilities to synthesise many valuable compounds [Stein 2005]. It has vigorous plant growth-promoting qualities (i.e., IAA and ABA), nitrogen fixation, siderophore production, phosphate and potassium solubilisation, and attributes like HCN synthesis as a biocontrol agent, enzymes, and antibiotics factory [Senthilkumar *et al.* 2009]. Various *Bacillus* species are involved in plant salt stress tolerance (Tab. 1); *Bacillus megaterium* increases *Zea mays* L. root tolerance and upregulates the Aquaporins (AQPs) genes [Marulanda *et al.* 2010], *Bacillus* spp. promote plant development, biomass, carbohydrates, and water homeostasis through phosphate solubilisation and siderophore synthesis [Khan *et al.* 2021; Rolli *et al.* 2015]. Using *Bacillus amyloliquefaciens*-SN13, plant biomass and the water content increase, while proline and ROS decrease in *Oryza sativa* L. [Chauhan *et al.* 2019]. *Bacillus aquimaris* enhances *Triticum aestivum* L. biomass, soluble sugars, and proline [Upadhyay, Singh 2015], while *Bacillus pumilus* raises antioxidants and decreased lipid peroxidation and SOD activity. In addition, *Bacillus aquimaris* enhances *Triticum aestivum* L. biomass while lipid peroxidation and SOD activity decrease [Jha, Subramanian 2014]. *Triticum aestivum* L. biomass, soluble sugars, nutrient uptake, and proline increase by *Bacillus megaterium, B. subtilis,* and *B. tequilensis* inoculation [Haroon *et al.* 2021; Talebi Atouei *et al.* 2019]. *Bacillus spp.* enhance *Capsicum annuum* L. fresh, dry weight, root length, proline, and antioxidant activities, and decrease ethylene in plants [Wang *et al.* 2018]. *Arabidopsis thaliana* L. nutrient uptake increased using *Bacillus amyloliquefaciens* [Liu *et al.* 2017].

d) AMF mitigates the saline conditions

Various communication processes between the plant and the fungus are facilitated by arbuscular mycorrhizal, which improves photosynthetic rates and increases water intake in high-stress environments [Birhane *et al.* 2012]. One promising method is the successful application of AMF to decrease salinity-induced plant damage [Fritz *et al.* 2022; Malik *et al.* 2022]. Plant growth is aided by AMF's establishment of a hyphal connection with plant roots, allowing roots access to soil [Bowles *et al.* 2016]. In addition, AMF improves the efficacy and delivery of a wide range of nutrients, improving nutrient use efficiency [Rouphael *et al.* 2015] (Fig. 4), enhancing soil quality by altering its structure and texture to promote plant growth and sustain plant health [Thirkell *et al.* 2017]. Moreover, critical physiological parameters are increased, such as the photosynthetic rate of total chlorophyll, consumption efficiency in leaves extract, and leaf water relations under water scarcity and salt conditions [Jerbi *et al.* 2022; Tisarum *et al.* 2022].

Furthermore, AMF inoculated *Allium sativum* plants grew better in saline conditions, with a greater leaf area index and fresh and dry biomass and N concentration in both shoot and root under saline stress [Borde *et al.* 2010; Parihar *et al.* 2022; Sharifi *et al.* 2007; Wang *et al.* 2018a, b]. The inoculated plants produced extra jasmonic acid, salicylic acid, and a variety of other essential inorganic nutrients. Total P, Ca^{2+}, N, Mg^{2+}, and K^{+} concentrations were more significantly increased in AMF-treated *Cucumis sativus* plants than in uninoculated plants under saline conditions [Hashem *et al.* 2018]. Inoculating the *Capsicum annuum* with mycorrhizal fungus enhanced chlorophyll content, Mg^{2+}, and N absorption while decreasing Na^{+} transport in saline environments [Çekiç *et al.* 2012]. In addition, Santander *et al.* [2019] discovered that mycorrhizal plants had higher biomass output, enhanced proline biosynthesis, improved N uptake, significant changes in ionic relations and significantly reduced Na^{+} storage for non-mycorrhizal plants. In addition, AMF applications can successfully manage the levels of essential growth hormones and minimise oxidative stress by lowering lipid membrane peroxidation under salinity stress [Hashem *et al.* 2016; Saxena *et al.* 2017]. Interestingly, plants treated with AMF also produced more organic acids, which up-regulated a saline-stressed plant's osmoregulation mechanism. For example, maize, wheat, and soybean plants produced more organic acids under saline conditions. In addition, AMF supported enhanced betaine biosynthesis, demonstrating that AMF indirectly functions in plant osmoregulation when plants are stressed by salinity [Ma *et al.* 2022].

CONCLUSIONS

Salinity harms agriculture (e.g., plant growth) by altering plants' essential biochemical and physiological functions. For example, salinity decreases photosynthesis efficiency and leads to an imbalance in plant phytohormones such as abscisic acid, cytokinin, and jasmonates, affecting the productivity of crops. In addition, plants have many mechanisms to survive under salt stress, such as ion homeostasis, antioxidant enzyme production, and hormone level regulation. Beneficial microorganisms such as *Bacillus* sp. and mycorrhizal fungi represent extraordinary abilities to synthesise a wide range of valuable compounds that decrease salt stress and promote plant growth. In sum, since salt stress is one of the most devastating abiotic stresses, it severely affects agricultural productivity in various ways.

It is necessary to cultivate and discover new salt-tolerant crops and employ different tools of biotechnology to identify salt tolerance genes and transfer them into economic crops. Consequently, much effort is needed to focus on the salt genes and transcription factors to add new salt-tolerant lines that can grow under extreme salt conditions.

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