ISSN: 2347-4688, Vol. 12, No.(2) 2024, pg. 545-563

Current Agriculture Research Journal

www.agriculturejournal.org

A Review of the Physio-Biochemical and Molecular Mechanisms of Salt Tolerance in Crop

PRAMOD VILAS SHELAR[1,2], GANESH DEEPAK MANKAR[1,3],
OM PRAFULL SONTAKKE[1], UTTAM RAMCHANDRA WAYASE[1],
KISHOR SURESH BHOSALE[3], GANESH CHANDRAKANT NIKALJE[4],
MAHENDRA LAXMAN AHIRE[6], TUKARAM DAYARAM NIKAM[5]
and RAJKUMAR BABAN BARMUKH[1*]

[1]Department of Botany, Modern College of Arts, Science and Commerce (Autonomous),
Shivajinagar, Pune, MH, India.
[2]Department of Botany, Haribhai V. Desai College of Arts, Science and Commerce, Pune, MH, India.
[3]Department of Botany, Nowrosjee Wadia College (Autonomous), Pune, MH, India.
[4]Department of Botany, Seva Sadan's R. K. Talreja College of Arts, Science and Commerce,
Ulhasnagar, Thane, Mumbai, MH, India.
[5]Department of Botany, Savitribai Phule Pune University, Pune, MS, India.
[6]Department of Botany, Yashavantrao Chavan Institute of Science (Autonomous), Satara, MS, India.

Abstract

Soil salinity is a major abiotic stressor that hampers agricultural productivity worldwide, with both natural and anthropogenic factors contributing to its rise. Salinity disrupts osmotic and ionic balance, impairs seed germination, hinders photosynthesis, and exacerbates oxidative stress, leading to significant membrane damage. In response, plants have evolved various biochemical and physiological and molecular mechanisms to tolerate high salinity. Recent research has greatly advanced our understanding of salt tolerance by identifying key genes associated with this trait. These studies have highlighted essential genes involved in ion transport, stress signaling, and maintaining osmotic balance. By integrating genetic insights with practical approaches like breeding and genetic engineering, researchers are developing crops better suited to saline environments, which is crucial for addressing global food security challenges. This paper aims to review recent findings on the impact of salt stress on plants and explore the physiological, biochemical, and molecular mechanisms underlying salt tolerance.

Article History
Received: 09 July 2024
Accepted: 27 August 2024

Keywords
Germination;
Growth Stage;
Oxidative Stress;
Osmolytes;
Plants Defence System;
Salinity Stress;
Salt Tolerance Genes.

CONTACT Rajkumar Baban Barmukh ✉ barmukhbotany@moderncollegepune.edu.in Department of Botany, Modern College of Arts, Science and Commerce (Autonomous), Shivajinagar, Pune, MH, India.

Doi: http://dx.doi.org/10.12944/CARJ.12.2.05

Introduction

Throughout their life cycle, plants and agricultural productivity are constantly subjected to various environmental challenges, which are key areas of scientific study. A variety of anthropogenic activities further intensifies these challenges.[1,2] To cope with environmental constraints, plants adopt various defence strategies. Plants are subjected to two types of stress: abiotic and biotic. Examples of abiotic stress include extreme temperatures (both high and low), strong winds, water surpluses and deficits, air pollution, UV rays, salinity, heavy metal deposits, mechanical damage, and chemical stressors.[1,2] Biotic stressors include weeds, predators, oomycetes, nematodes, and herbivores.[1,2]

One of the main abiotic factors that lower agricultural output is salt stress, which affects seed germination, early seedling growth, and both vegetative and reproductive growth. One of the main factors limiting the amount of agricultural output available to feed a growing population is salt stress.[1,2] Due to human activity, salt stress is already present on between 20 and 50 percent of cultivable land worldwide,[1,2] Furthermore, because of inadequate irrigation, excessive surface evaporation, weathering of local rocks, little rainfall, and bad agricultural methods, saline land is growing by roughly 10% a year.[3] 32 million hectares of agricultural land and over 800 million hectares of other land are salinized worldwide.[4] However, one of the biggest obstacles to global agriculture will be the need for 70% more food to feed the world's population when it grows to 2.3 billion by 2050.[5] Stresses other than salt stress account for over half of yield losses.[6] Nearly 90% of plant-based food comes from thirty mostly salt-sensitive crops. According to published research, a substantial yield loss happens at intermediate salinity levels, about 40–80 mM NaCl.[7]

Ions in saline soil impose osmotic stress that later results in ionic stress.[8,9] Salinity in the soil has an impact on seed germination, early plant seedling growth stages, and total crop output and production limitations.[8,10,11] Photosynthesis is an essential cellular metabolic process needed to produce food for plant survival.[12] Salinity affects the photosynthesis process leading to cell and even plant death.[13,14] Plants experience oxidative stress as a result of soil salinity, which creates reactive oxygen species (ROS) that damage cell biomolecules.[15] These ROS can cause membrane damage by lipid peroxidation.[16] Salt stress tolerance is the capacity to endure high salinity environments. The osmotic and ionic balances both within and outside of cells are mostly upset by salinity. Therefore, by carefully regulating their ion intake and compartmentalization, plants preserve ion homeostasis.[17] To maintain osmotic balance, plants produce several osmolytes.[18] Plants have evolved an antioxidant defence system of enzymatic and non-enzymatic antioxidant molecules in response to the overproduction of ROS.[19,20]

Salt stress represents a major challenge for agriculture worldwide, prompting significant research into plant mechanisms for coping with salinity. Recent studies have provided valuable insights into the genetic and molecular bases of salt tolerance.[21] Various genes which are expressed under salinity were found by Kim and Kim (2023) in rice,[22] by Liu (2022) in mungbean,[23] by Irshad (2022) in wheat[24] and by Qi X. (2014) in soybean.[25] It was suggested that identified genes were involved in Osmolyte productions, antioxidant defence system, secondary metabolite synthesis.[24] Together, these studies underscore the progress in identifying genetic targets and devising strategies to enhance salt tolerance. By merging genetic discoveries with practical applications, such as gene engineering and breeding, researchers are advancing towards developing crops that can better withstand saline conditions. Ongoing research and technological innovations are crucial for translating these findings into effective solutions that enhance agricultural productivity under salt stress.

Types and Causes of Salinity

Natural or Primary Salinity

Geological, hydrological, and pedological processes accumulate salts responsible for natural, i.e., primary salinity. Natural saltiness is the result of two main natural processes. First, there is the weathering of parent rocks such as igneous rocks (such basalt and phenolates), which contain soluble salts of different kinds (mostly Na, Ca2+, and Mg2+ chlorides, and to a lesser degree, SO4− and HCO3−).[26] The second is the oceanic or cyclic salts that are deposited by rainfall after being transported by the wind and landing on land, such as sodium chloride.[27]

Human-Induced or Secondary Salinity

Secondary or human-induced salinity is the result of human activity and includes things like overgrazing, incorrect irrigation techniques, deforestation, wastewater emissions from cities or industry that include salt, and chemical fertilisers used in agriculture. Salt accumulation occurs in the soil when soluble salts from surface and groundwater are continuously used to irrigate agricultural area with inadequate drainage systems.[28] It brings salts above ground through the upward movement of water. Eventually, when surface water evaporates, it leaves behind salt, which increases soil salinity. Replacement of native vegetation with crops like cereals with shallow roots results in less evapo-transpiration, and more leaching causes rising of groundwater level.

Effects of Salt Stress on Plants

Salinity generally results in an imbalance of water and ions, disruption of the cell membrane, restriction of the detoxification process of reactive oxygen species (ROS), reduction of antioxidant enzyme activity, and reduction of photosynthetic activity.[29] Production of reactive oxygen species (ROS) in response to salinity causes oxidative stress, which breaks down essential plant cell activities and deteriorates macromolecules like lipids, proteins, and DNA.[30] The synthesis of photosynthetic pigments and photosynthesis, germination, growth, protein synthesis, nucleic acid synthesis, lipid metabolism, and secondary metabolite production are all impacted by salt stress, which also induces oxidative and osmotic stress.

Osmotic Stress and Ionic Imbalance

Poor plant growth and development are the result of excessive salt's first osmotic or water-deficit effect, which is followed by ionic stress or ion toxicity.[31] High salt accumulation in the soil and plant tissues during the first stage of salinity, also known as hyperosmotic stress, results in osmotic stress, reduces the ability of the root system to absorb water, and increases leaf water loss.[32] Ionic stress is caused in the latter phase by the build-up of salt ions like Na+ and Cl−. Growth and development are impeded by high concentrations of Na+ because they prevent the absorption of K+ ions, one of the required components. An overabundance of Na+ and Cl- ions causes an ion imbalance, which may result in physiological problems.

Germination

One of the crucial stages in a plant's life cycle that ultimately determines production is seed germination. Nonetheless, salt stress poses a serious threat to this stage.[25] The main stressor that causes germination to be delayed and the percentage of seeds that germinate to be reduced is salinity.[33] Excessive levels of salt in the soil lower the osmotic potential of the soil water, which in turn lowers the amount of water that dry seeds can absorb. Additionally, ionic stress and ion toxicity are brought on by the intake of excessive Na+ and Cl-ions, which impair vital metabolic functions like respiration, energy synthesis, and the metabolism of proteins and nucleic acids.[34] Salinity reduces reserved food, protein synthesis, and water potential in many plant seeds that germinate, including broccoli and cauliflower.[35]

Under typical environmental circumstances, the germination process of seeds proceeds through three stages. Stage I is the imbibition stage, during which dry seeds quickly absorb water. Stage II is the plateau stage, during which time cellular metabolic systems are reactivated and water uptake is inhibited. Water is constantly absorbed during stage III, the post-germination stage, until germination is fully completed (Figure 1). Under salinity, osmotic stress in stage I, ionic stress in stage II, and a combination of osmotic and ionic stress in stage III are responsible for inhibiting or delaying seed germination.[36]

During the seed germination period, salinity induces an imbalance in hormones, particularly in abscisic acid and gibberellin, which delays and occasionally even inhibits seed germination. Reactive oxygen species (ROS) are produced more readily in salinity. Simultaneously, decreased ROS scavenging causes the cells' vital macromolecules—proteins, nucleic acids, lipids, and carbohydrates—to be damaged, which inhibits the process of seed germination.[37] Salinity has negatively affected the germination in soybean,[38] Medicago sativa,[33] and Hordeum vulgare[34]

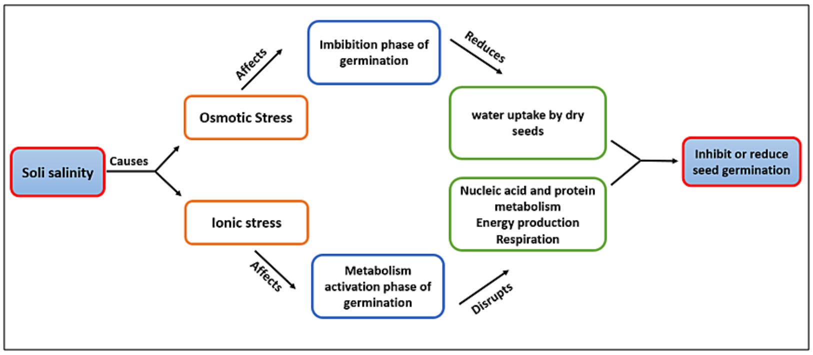

Fig. 1: Effect of salinity on seed germination

Plant Growth

Ion toxicity and osmotic pressure both have an impact on plant growth under salinity. Plant development is inhibited by salt because of increased osmotic potential and matrix in the soil, which reduces water intake.[39] Plant growth and development are impacted by high salinity, which causes the plant to become stunted.[11] The life and growth of the plant depend heavily on the seedling stage, the first stage of plant establishment. On the other hand, salinity has a significant impact on the seedling stage, which results in reduced plant growth.[40] An immediate effect of high salinity is the reduction in leaf expansion[11,40] As salt concentration rises, salinity also affects and decreases leaf area, plant height, shoot length, root length, fresh weight, dry weight, and tissue water content.[38,41] Sahin (2018)[39] have also observed that vegetative growth parameters such as plant height, plant biomass, stem diameter, leaf area are significantly reduced under salinity at all salt treatments compared to control in *Brassica oleracea.* Furthermore, they discovered a strong negative linear association (almost 90%) between the parameters of vegetative growth and salinity. Under salinity, there were also fewer secondary roots.[38]

Crop yield

Abiotic stresses reduce crop yield and production.[9] Due to poor water irrigation techniques and insufficient drainage of irrigated agricultural fields, which cause salt build-up in the soil and decrease water and nutrient intake, salinity restricts the growth of crop plants, mostly in arid and semi-arid regions.[42] About 30 crop species such as rice, sorghum, barley, maize, wheat, sugarcane, potato, sugar beet, soybean, sweet potato, cotton, and mungbean provide 90% of plant-based human food. At moderate salinity conditions (EC 4-8 dS/m), 50-80% yield loss was observed in these crops.[43] If salinity increases in the initial phase of the plant's life cycle, the plant growth, development, yield, and production are significantly reduced, and the quality and quantity of the produce are compromised.[42] Maas and Hoffman (1977) 44 have published a model that suggests that relative crop yield is never reduced until a certain threshold level of salinity is exceeded. Loss in crop yield due to salinity has an economic impact on agriculture and bio-based industries. According to reports, irrigated agricultural lands lose more than 27 billion US dollars annually due to salt in the soil.[45] Various studies have reported differences in yield loss at different salinity levels. Corn, wheat, and cotton showed yield losses of 55%, 28%, and 15% at salinities of 8 to 10 dS/m, respectively. In cotton, the 18 ds/m salinity results in a 55% yield reduction.[46] Growing salt in mungbean caused a decrease in the pod parameters (number of pods/plant, average pod length, fresh and dry weight of pod/plant) and seed parameters (number of seeds/plant, weight of 100 seeds, and seed yield/plant).[47] Less green leaves, poor leaf expansion, a smaller number of leaves, and leaf senescence result in less photosynthetic activity, maybe the reason behind the reduction in yield under salinity. Some research has shown that as salt content increased, wheat production, spike length, spikelet count, and spike/1000 grain weight decreased.[48] They concluded that yield reduced immediately under salinity due to osmotic and ionic stress.

Photosynthesis and Photosynthetic Pigments

Plants produce their food by one of the important metabolic processes, photosynthesis, which helps accumulate dry matter and productivity. Salt stress disrupts and limits photosynthesis either by stomatal closure, leading to reduced intercellular CO_2 concentration or non-stomatal limitations.[13] Short-term salt effects on photosynthesis are visible within a few hours to one or two days, stopping carbon assimilation in plants. Long term effect of salt on photosynthesis occurs after a few days.[11] Salt stress affects the ultrastructure of a chloroplast. Disruption of thylakoid structure, increment in size and number of pellets of the plastid and decreased amount of starch, aggregation of chloroplast without stroma and grana in leaves was evident under salt stress.[49] Numerous factors contribute to the reduction of photosynthetic activity under salinity, including changes in enzyme activities, osmotic stress resulting in a decrease in the osmotic potential of water in the soil, disruption of the photosynthetic electron transport system, and dehydration of membranes reducing CO_2 permeability. Also, the ion toxicity of salts reduces the uptake of essential nutrients, limiting photosynthesis and generating reactive oxygen species (ROS).[50] Salinity affects receptors of photosystem II (PSII) of light-dependent reaction, which reduces the density of active reactions centres.[51]

Plant pigments harvest sunlight and offer photosynthetic protection in the light reaction of photosynthesis. Leaf photosynthetic pigments are vital for photosynthesis and gross primary production. The chlorophyll content represents the plant's photosynthetic capacity.[52,53] Carotenoids composed of carotenes and xanthophylls are other major photosynthetic pigments. Carotenoids are an essential structural component of a photosynthetic antenna that harvest light energy.[54,55] Carotenoids not only aid in photosynthesis but also function as antioxidants and have been shown to scavenge reactive oxygen species.[55] Carotenoids also protect reaction centres by dissipating excess light energy absorbed during photosynthesis.[56] The chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids were reduced under salinity in salt-sensitive lines of *Medicago truncatula.* Over accumulation of Na^+ ions in leaf tissue causes changes in chlorophyll pigments and limits their synthesis, leading to leaf chlorosis.[57] Decreased chlorophyll and carotenoid contents under salinity were observed in cotton[58] and soybean.[59] In plants under stress from salt, the breakdown of chlorophyll pigments is caused by the enzyme chlorophyllase.[59]

Oxidative Stress

Reactive oxygen species (ROS) are continuously produced by plants during respiration and photosynthesis, and these can harm cells oxidatively.[60] Therefore, in order to shield plant cells from oxidative damage, plants need to scavenge these ROS. Enzymatic and non-enzymatic antioxidants are involved in two different ROS scavenging systems in plants.[61] The generation of ROS and its scavenging in plant cells are in equilibrium in the natural world. Oxidative stress, however, results from many environmental pressures upsetting this balance.[62]

ROS are oxygen radicals or their derivatives such as hydroxyl radical (•OH), superoxide (O_2•), singlet oxygen ($1O_2$) and hydrogen peroxide (H_2O_2), ozone (O_3), hypoiodous acid (HOI), hypochlorous acid (HOCl), hypobromous acid (HOBr), perhydroxy radical (HO_2•), peroxyl (RO_2•), peroxy radical (ROO•), semiquinone (SQ•-), and carbonate (CO_3•-). ROS damages the cell membrane and cell organelles in several cell organelles, including the chloroplast, mitochondria, endoplasmic reticulum, peroxisomes, plasma membrane, and cell wall, when exposed to harsh environmental conditions like salt. Excess ROS are produced as a result of osmotic and ionic stress, nutritional imbalance, and other related downstream consequences caused by salt stress.
ROS produced by salinity are hazardous and can harm proteins, lipids, and nucleic acids. These ROS cause these biomolecules' roles to shift, which in turn causes physiological and biochemical changes in cells that ultimately result in oxidative stress.[63] However, plants' antioxidant defensive system, which consists of both enzymatic and non-enzymatic components, helps them scavenge or detoxify excess ROS, thereby reducing oxidative stress.[64] Antioxidant enzymes including catalase, peroxidase, superoxide dismutase, and ascorbate (ASC)–glutathione (GSH) cycle enzymes make up the enzymatic antioxidant system. (ascorbate peroxidases, dehydroascorbate reductase, monodehydroascorbate reductase, glutathione reductase, glutathione-s-transferases, glutathione

peroxidases),[61,65] Scavenging or mitigating ROS created during oxidative stress are non-enzymatic antioxidants such as glutathione, ascorbate, vitamin E, carotenoids, flavonoids, phenolics, and non-protein amino acids like proline.[63,66,67]

Membrane Damage

Plant membranes are an important protective biological barrier of plant cells, protecting the internal contents of cells and organelles from abiotic and biotic stresses. These membranes are made up of lipids and proteins and play an important role in transporting substances, transmitting energy, and transducing signals. Further, selective permeability of cell membranes for ions helps regulate ion homeostasis inside a cell. Changes in the structure and functions of membrane lipids are observed under salinity in halophytes and glycophytes alike. Salinity-induced overproduction of ROS causes oxidative stress through increasing relative permeability and decreasing fluidity of membranes. It also affects selectivity, flow rate, and transportation of ions, alters properties of membrane proteins, signalling molecules, and signal transduction. Moreover, it also causes osmotic stress due to exosmosis of many electrolytes.[16,68]

One of the main results of lipid peroxidation, malondialdehyde (MDA), has the ability to modify and deactivate the proteins and enzymes that are found on the plasma membrane, changing the structure and functionality of the membrane. MDA content is also the primary indicator of plasma membrane damage under salinity. Momeni (2021) have reported significantly increased MDA content in salt-sensitive durum wheat genotype compared to salt-tolerant type.[69] Lipid peroxidation found in cellular and organellar membranes increases when ROS are overproduced in plant cells, affecting the cell's function. Lipid peroxidation causes damage to DNA and proteins.[70] ROS accumulation, membrane damage, and imbalanced ion homeostasis hamper the rate of protein synthesis, It causes toxic substances and amino acid buildup inside the cell. Toxic polyamines like glutamine and butane diamine are produced from amino acids including arginine, isoleucine, and ornithine. Plant growth and development are severely harmed by the buildup of these poisonous chemicals.[71]

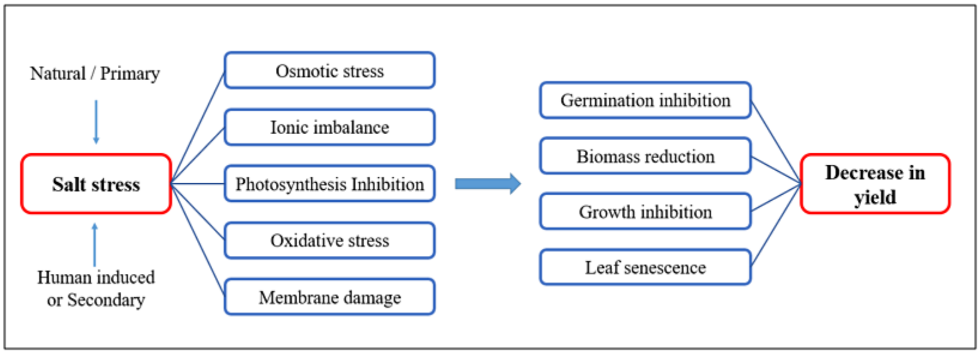

Fig. 2: Impact of salt stress on the plants

Salinity Tolerance in Plants

Plants have a complex procedure for adjusting to salt that incorporates numerous processes. The capacity of a plant to complete its life cycle with enough growth and output is known as salinity tolerance.[72] Three main ways that soil salinity impacts plant growth and development are through osmotic stress, ion toxicity, and nutrient uptake and translocation.[40] Plants are divided into two categories: halophytes (very salt-tolerant) and glycophytes (salt-sensitive). Halophytic plants regulate the ion levels in their shoots and leaves and limit ion uptake through their roots as one of several adaptations they make to withstand salinity.[72] By altering their morphological, anatomical, physiological, and biochemical processes, halophytes also prevent salt stress.[73]

Generally, plants have systems to withstand saline in the soil. First, plants have a mechanism called salt avoidance that keeps salt away from tissues or cells that are metabolically active.[9] It includes ion dilution, active ion exclusion using ion pumps, and passive ion exclusion using a permeable membrane.[40] Secondly, through ion compartmentalization in vacuoles of plant cells.[74] Therefore, the mechanism of salt tolerance may include a) controlled ion uptake, b) tissue level tolerance, c) compartmentalization of ions in a vacuole, d) discrimination of ions, and e) synthesis of osmolytes, hormones, and antioxidant enzymes.[9]

Ion Homeostasis and Compartmentalization

Ion homeostasis is one of the most crucial defence systems for a plant's regular growth in salty environments because salinity stress throws off the usual ion balance inside a cell. Numerous plants have evolved effective systems to preserve ion homeostasis in the cytoplasm of their cells by controlling ion intake and compartmentalization to maintain low cytoplasmic ion concentrations. Halophytic and glycophytic plants cannot withstand or tolerate higher salt concentrations in the soil. Hence, they transport excessively accumulated ions to vacuoles or compartmentalize the ions in different tissues that are ultimately sacrificed to protect the plant from damage due to salinity.[75,76] Certain ions, such as calcium, potassium, and nitrogen, are necessary for the plant's growth and development. These ions are found in soil, but they compete with other ions at higher concentrations to enter plant cells. Salt ions cause an imbalance in the absorption of ions necessary for plant development. Ion transit and low concentration are essential functions of cell membranes.

Ions are transported inside plants through the membrane proteins such as ion channel proteins, symporter, and antiporters present on the cell membrane.[77] NaCl is the main salt present in saline soil; hence the study of exclusion of Na^+ from roots, long-distance Na^+ transport mechanism, and compartmentalization of Na^+ ion is a crucial area of research to understand ion homeostasis at tissue and cell level. Na^+ toxicity in a cell is controlled through Na^+/H^+ antiporters present on the vacuolar membrane. These antiporters help sequestration of excess Na^+ in the vacuole under salinity. Vacuolar Na+ sequestration prevents the increase of Na^+ and maintains the Na^+/K^+ ratio in the cytosol.[78] Vacuolar membranes contain two primary antiporters: vacuolar pyrophosphate (V-PPase) and vacuolar-type H+-ATPase (also known as V-ATPase).[76] For Na^+ sequestration in vacuoles, the most well-known transporters are NHX1 Na+, K+/H+ exchanger, and Na+.[79,80]

Under salinity, the salt-overly-sensitive (SOS) signalling system preserves ion homeostasis. It comprises plasma membrane SOS3, SOS2, and SOS1-like Na+/ H+ exchangers. These SOS exchangers extrude Na+ from the root cells to maintain ion homeostasis and increase salt tolerance.[81] Under typical circumstances, the cytoplasm of the cell maintains a K+ concentration of up to 100 mM. Maintaining this cytosolic K^+ concentration for plant growth and development is crucial. However, this K^+ homeostasis is disturbed under salinity, altering critical physiological processes dependent on K+ concentration.[82] Under salinity, Na^+ concentration is increased in soil; hence, because of similar charges, Na+ competes with K^+ for the same transporter, which ultimately reduces K^+ uptake.[9] It is well known that Ca^{2+} also helps during salinity stress which reduces the toxic effect of NaCl stress by facilitating higher K+/Na+ selectivity.[83] Cytosolic Ca^{2+} increases under salt stress and is transported from the apoplast and intracellular compartments. As a result, there is less salt stress on plant growth and development since the subsequent rise in Ca^{2+} starts signal transduction.[84]

Osmo-Protection

Stressful environmental circumstances cause plants to build large amounts of cellular osmoprotectant, which is crucial to their defence mechanisms. These osmolytes are tiny, electrically neutral, organic, low molecular weight, and extremely water-soluble substances. Moreover, osmoprotectant are nontoxic to plants at high concentrations under unfavourable environmental conditions due to their involvement in intracellular metabolisms operating under stress conditions.[85] Three main types of osmolytes are recognized: a) amino acids (proline, gamma-aminobutyric acid (GABA), hydroxyproline, pipecolic acid, and polyamines), b) betaines and associated molecules (glycine betaine, proline betaine, and alanine betaine), and c) sugars (sucrose, trehalose, sorbitol, fructan, and raffinose) and polyols (mannitol and inositol).[85,86]

These osmolytes accumulate during stress conditions for the cell's survival and maintain the osmotic balance between cell cytoplasm and surroundings.[61] In addition to osmotic osmoregulation, osmoprotectant also help to maintain cellular turgor pressure, scavenge reactive oxygen species, stabilise enzymes or proteins, preserve membrane integrity, replenish inorganic ions, reduce ion toxicity, and safeguard cellular components.[86,87] Moreover, osmoprotectant regulate protein folding, photosynthetic upregulation, and activation of defence-related genes under various stress conditions.[87,88]

Proline

One of the important osmolytes that accumulates in the cytoplasm under salinity is proline. It is highly capable of hydrating. Its hydrophobic ends attach to proteins, whereas its hydrophilic end can attach to a water molecule. Because proteins bound to proline may bind more water molecules, they help fend off dehydration and stress-induced protein breakdown. When there is stress, proline synthesis rises and its breakdown falls.[89] It functions as a signalling molecule that helps keep proteins, enzymes, and membranes stable. Proline upregulates membrane proteins to maintain membrane integrity, scavenges reactive oxygen species, and maintains the balance of ion homeostasis under salinity. Many studies have shown that proline increases water uptake, enhances the activity of antioxidant machinery, and reduces the accumulation of toxic ions under salinity. Proline also acts as a molecular chaperon that can maintain protein folding and confirmation. It can also buffer cytosolic pH and balance the redox condition.[31,90] Proline can mitigate the effect of stress in two ways: a) by accumulating an excess of proline under stress by upregulating its biosynthesis, which can serve as an osmolyte, chaperone, and as a direct scavenger of ROS, and b) by activating metabolic flux of proline which is linked to other mechanisms in plants. This proline metabolic flux helps maintain cellular energy, NADP+/NADPH balance, and activate signal transduction that promotes cell survival.[89]

Glycine Betaine

A quaternary ammonium molecule called glycine betaine helps mammals, fungus, algae, bacteria, cyanobacteria, and members of the Poaceae and Chenopodiaceae families lessen the harmful effects of various abiotic stressors. Most importantly, as an osmolyte under salinity, it protects higher plants from stress damage.[91] Glycine betaine has a unique structure that can bind with hydrophilic and hydrophobic ends of enzymes and proteins present in plants. Thus, it prevents enzymes and proteins from denaturation and retains membrane integrity, osmotic balance, and scavenges ROS under stress conditions.[86,92] Glycine betaine, which is produced in the chloroplast of flowering plants, aids in the defence of proteins, enzymes, and thylakoid membranes in the photosynthetic machinery during stressful situations.[92] Syeed (2021).[93] have reported that glycine betaine protected membrane damage and increased antioxidant defence system that enhanced the photosynthetic activity and plant growth. Glycine betaine regulates the osmotic balance in stressed plants and helps ion transporters for normal functioning. Hence, glycine betaine is considered a protective compound that discriminates Na^+ against K^+ under salinity. Glycine betaine is thought to increase the vacuolar efficiency of root cells to accumulate and store more Na^+ ions under salinity. They have also reported increased antioxidant (enzymatic and non-enzymatic) activity after exogenous application of glycine betaine under salinity that helped in scavenging ROS.[94]

Amino Acids

In order to create stress tolerance in plants, free amino acids are a key solute for osmotic adjustment in high salinity environments.[40] Amino acids including glycine, alanine, proline, isoleucine, leucine, valine, arginine, glutamine, asparagine, and non-protein amino acids like pipecolic acid, citrulline, ornithine, and gamma-aminobutyric acid accumulate in cells as a result of desiccation under stress.[92] One of the main amino acids that rises in salinity is proline.[95]

Sugars and Sugar Alcohols

Plants undergo dehydration or desiccation under salinity due to osmotic stress. Sugar and sugar alcohols maintain the osmotic equilibrium of cells under dehydration. Plants synthesize and accumulate various monosaccharides, disaccharides, and other sugars such as glucose, fructose, sucrose, fructans, and starch to minimize salinity-induced osmotic stress.[96] Sugar molecules replace their hydroxyl group with water molecules under dehydration and maintain a hydrophilic structure in their hydrated orientation.

Under severe desiccation, these sugars may substitute for water-bound macromolecules, thereby maintaining hydrogen bands. Thus, they prevent protein folding and membrane disturbance.[97,98]

Plants also synthesize sugar alcohols such as mannitol, sorbitol, and inositol under salinity stress to improve salt tolerance by osmotic adjustment. By promoting development, scavenging ROS, preserving cell turgor, and securing Na^+ inside vacuoles, they lessen stress.[99]

Antioxidant Defence System

Plants produce an excess of ROS under salinity which can damage the cell. Hence, to scavenge ROS, plants have adapted an antioxidant defence mechanism. The two primary categories of antioxidants in this process are: 2) Non-enzymatic antioxidants such as carotenoids, alkaloids, flavonoids, glutathione, ascorbic acid, and α-tocopherol; and 1) enzymatic antioxidants such as catalase, ascorbate peroxidase, glutathione peroxidase, superoxide dismutase, monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase.[20]

Enzymatic Antioxidants

Superoxide dismutase (SOD) is the most critical and effective omnipresent metal-containing enzymatic antioxidant in plants. Plant stress tolerance is increased as a result of it serving as the first line of defence against oxidative stress. Superoxide radical (O-2) is broken down by SOD into oxygen (O2) and hydrogen peroxide (H2O2). SOD has three types of isozymes based on SOD-binding metal ions: a) Cu/Zn- SOD localized in chloroplast, cytoplasm, and peroxisomes, b) Fe-SOD localized in chloroplast, and c) Mn-SOD localized in mitochondria.[100] Butt (2021) observed that when chilli plants were salinized, SOD activity increased.[101]

Catalase (CAT) was the first enzyme discovered to play a role in the antioxidant defence system. CAT functions as a scavenger of H2O2 produced in peroxisomes during photorespiration and the β oxidation of fatty acids.[102] CAT specifically decomposes H_2O_2 into H_2O and O_2 with a very high turnover. In angiosperms, three CAT genes are studied which express isozymes- CAT1, CAT2, and CAT3. Peroxisomes and glyoxysomes are the primary locations for these isozymes. CAT activity was elevated under salinity in barley[103] and chili.[104]

Peroxidase (POD) is a family of isozymes, heme-containing monomeric glycoproteins, that oxidize various molecules by utilizing H_2O_2. H_2O_2 acts as an electron acceptor and is converted into $2H_2O$. POD is localized in the cell wall, cytoplasm, vacuoles, and organelles of the plant cells.[104] Increased POD activity under salinity was reported in *Dracocephalum moldavica*[64] and chili.[101]

Compared to SOD and CAT, ascorbate peroxidase (APX) has a greater affinity for H2O2. It is essential to the cycles of glutathione (GSH) and ascorbic acid (AsA). In an APX-catalysed reaction, ascorbic acid acts as a reducing agent, which reduces H2O2 to 2H2O. There are five isozymes of APX found in different organelles: cytosol, mitochondria, peroxisome thylakoid, and the stroma of plant cells.[105,106] Kharui (2019) found that under salinity, the salt-tolerant "Umsila" date palm showed more APX activity than the salt-sensitive "Zabad" date palm.[66] ROS scavenging is not a direct function of other antioxidant enzymes like glutathione reductase (GR), dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR). They do, however, play a role in the AsA and GSH cycle's renewal. This AsA-GSH cycle ultimately detoxifies H_2O_2 and reduces oxidative damage.[107] Glutathione peroxidase (GPX) protects the cell from oxidative stress by using glutathione thioperoxide with the help of glutathione S-transferase (GST).[108,109]

Non-Enzymatic Antioxidants

One of the main substrates for ROS detoxification in both stressful and non-stressful situations is ascorbic acid (AsA), also known as vitamin C. It is a low molecular weight, water-soluble antioxidant molecule. It is one of the most potent antioxidants due to its regenerative nature.[110] AsA acts like a co-enzyme that donates electrons to scavenge ROS. It also regenerates vitamin E, which acts as an antioxidant.[111] The AsA- GSH pair regulates many developmental processes in plants by manipulating oxidative metabolism.[110] Noreen (2021) shown that barley's antioxidant defence system improved following ascorbic acid foliar fertigation in a salinity-sensitive environment.[111]

Glutathione, also known as γ-glutamyl-cysteinyl-glycine, is a thiol molecule with a low molecular weight that is soluble in water. By directly or indirectly detoxifying ROS, it regulates intracellular defence in a crucial way.[112] Additionally, it is important for the AsA-GSH cycle, which detoxifies ROS.[107] Kharusi (2019) reported enhanced glutathione accumulation under salinity in a salt-tolerant cultivar of date palm compared to a salt-sensitive one.[66]

Carotene (CAR) is a lipid-soluble antioxidant pigment present in chloroplast. It primarily acts as a light-harvesting accessory pigment and is also known to detoxify ROS in plants. Under stressed conditions, carotenoids react with triplet chlorophyll (3Chl*) or activated chlorophyll molecule (Chl*), thus preventing the formation of singlet oxygen and other ROS, thus protecting photosynthetic apparatus.[113] Ben-Abdallah (2019) reported increased carotenoid content in *Solanum villosum* at 100 mM sat stress.[114] Moreover, they found enhanced expressions of genes related to carotenoid production, such as phytoene synthase 1, phytoene synthase 2, and b-lycopene cyclase.

Alpha-tocopherol (Vitamin E) is also known to scavenge the ROS derived from photosynthesis, mainly singlet oxygen and hydroxyl radicle. It scavenges lipid peroxy radicals and prevents lipid peroxidation in the thylakoid membrane, thus protecting plants from oxidative damage under stress. Its level is regulated by plant sensitivity and severity of stress.[115] Other non-enzymatic antioxidants such as flavonoid, mannitol, and proline also help to scavenge ROS in plants.[67]

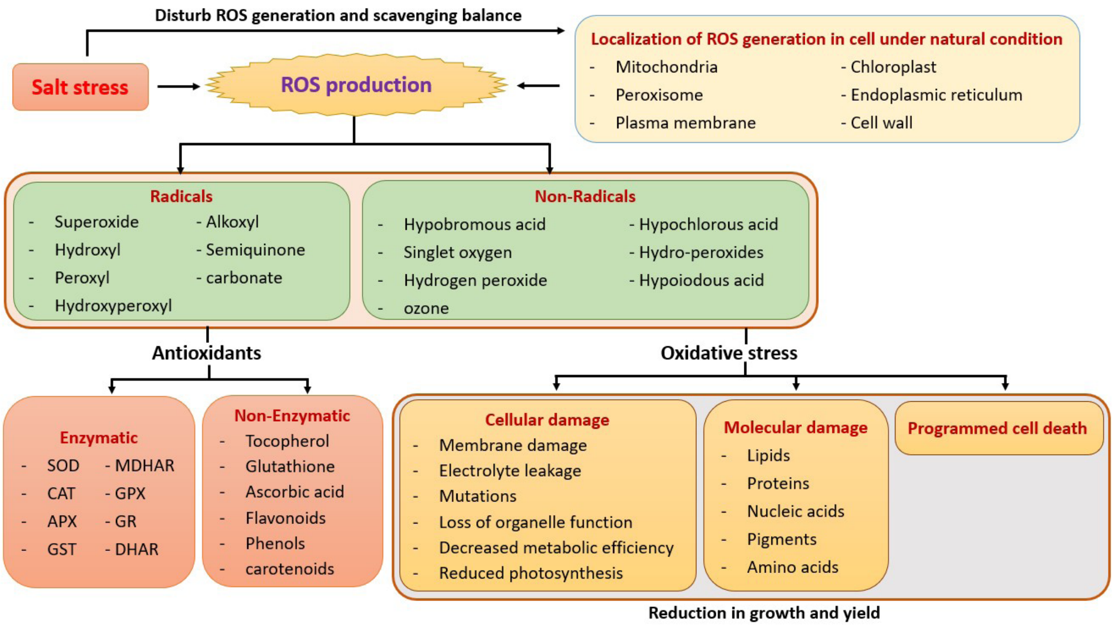

Fig. 3: An overview of antioxidant defence and oxidative stress in relation to salt

Salt Tolerance Genes in Plants

Salinity is one of the most challenging abiotic factors affecting plant growth and productivity, especially in arid and semi-arid regions. The ability of plants to tolerate salt stress is a complex trait governed by a range of genes and mechanisms. Advances in molecular biology and genomics have significantly enhanced our understanding of the genetic foundations of salt tolerance in plants, paving the way for the development of salt-resistant crop varieties. This section highlights key findings from recent studies on plant genes responsible for salt tolerance, with a focus on the integration of transcriptomic, genomic, and functional approaches. Gaining insights into the genetic basis of salt tolerance is essential for the development of salt-resistant crops. Numerous studies have investigated the molecular mechanisms and genes linked to salt tolerance, offering a deeper understanding of how plants adapt to saline conditions.

Molecular Mechanisms of Salt Tolerance

Salt stress in plants initiates a series of intricate physiological and molecular responses. To combat the harmful effects of salt stress, plants employ mechanisms such as ion homeostasis, osmotic regulation, and the activation of specific stress-responsive signaling pathways.[31] Rice, a crucial crop highly susceptible to salt stress, has been the subject of various studies. In a comprehensive approach, Kim (2023) identified potential salt tolerance genes in rice seedlings by combining transcriptome analysis with Genome-Wide Association Study (GWAS).[22] This research successfully pinpointed several genes associated with salt tolerance, including those involved in signalling pathways, ion transport, and stress responses. The study illustrates the effectiveness of integrating GWAS and transcriptome data to unravel the genetic complexities of salt tolerance in crops, providing valuable targets for rice breeding programs aimed at enhancing salt tolerance.[22] Yang and Guo (2018) conducted a comprehensive analysis of the molecular networks and signaling pathways involved in salt stress response, identifying key regulatory genes associated with ion balance, antioxidant defense, and osmotic regulation.[116] These genes are often controlled by complex signaling cascades involving calcium-dependent protein kinases (CDPKs), mitogen-activated protein kinases (MAPKs), and transcription factors such as MYB and NAC.[117] Gaining insight into these pathways is crucial for developing strategies to enhance salt tolerance through molecular breeding or genetic engineering.[118]

Yang and Guo (2018) detailed the molecular mechanisms involved in plant responses to salt stress, particularly focusing on key signaling pathways like the SOS (Salt Overly Sensitive) pathway, which plays a critical role in maintaining ion balance by regulating sodium (Na^+) ion transport.[116] They also underscored the dual role of reactive oxygen species (ROS) as both signaling molecules and potential sources of cellular damage if not properly managed.[31]

Athar (2022) reviewed the role of various salt stress proteins in plants, highlighting the importance of proteins such as dehydrins, LEA (Late Embryogenesis Abundant) proteins, and aquaporins.[119] These proteins are essential for osmotic regulation, protection of cellular components, and maintaining water balance under saline conditions.[119]

Understanding the genetic basis of salt tolerance necessitates an in-depth exploration of the molecular mechanisms underlying plant responses to salt stress. In a similar vein, Razzaque (2019) explored gene expression changes in a reciprocally crossed rice population subjected to salt stress.[117] Their analysis identified genes with differential expression patterns linked to salt tolerance. These findings underscore the genetic variability in how plants respond to salt stress, offering valuable insights for breeding strategies aimed at enhancing salt tolerance in rice.

Salt Stress Proteins and their Functional Roles

Proteins play a crucial role in regulating how plants respond to salt stress. Athar (2022) provided an in-depth review of these stress-related proteins, highlighting their various functions, including the scavenging of reactive oxygen species (ROS), facilitating ion transport, and maintaining osmotic balance.[119] The review underscored the importance of specific proteins, such as SOS (Salt Overly Sensitive) and HKT (High-affinity K+ Transporter), in maintaining ion homeostasis under salt stress. Identifying and characterizing these proteins not only provides insight into how plants adapt to saline conditions but also offers potential targets for improving salt tolerance in plants.

Gene Expression Under Salt Stress

Investigations into gene expression have significantly advanced our understanding of salt tolerance in plants. Razzaque (2019) performed a gene expression study on a reciprocally crossed rice population exposed to salt stress.[117] Their findings revealed that several genes associated with ion transport, stress signaling, and metabolic pathways were differentially expressed under saline conditions. These insights underscore the critical role of gene expression studies in elucidating the genetic mechanisms of salt tolerance and provide valuable information for developing rice varieties with improved resistance to salt stress.

Genetic Engineering for Enhanced Salt Tolerance

The field of genetic engineering has introduced new strategies for boosting salt tolerance in plants through the incorporation of salt-tolerance genes from various species. Munns (2005) explored the integration of these genes, emphasizing the need to combine physiological traits with genetic modifications.[118] He suggested that a comprehensive understanding of the genetic basis of salt tolerance, along with the combined effects of multiple genes, could facilitate the development of crops resilient to saline conditions. Additionally, Zamanzadeh-Nasrabadi (2023) reviewed the potential of bacterial genes in augmenting plant salt tolerance.[120] They noted that incorporating bacterial genes could enhance osmolyte production, ion transport, and stress signaling, thus improving plant endurance under saline stress.

Conclusion and Future Perspective

Salinity poses a significant challenge globally, as it adversely affects the growth and development of plants and crops, leading to reduced yields and diminished agricultural productivity. The increasing salinization of soil, driven by both human activities and natural processes, exacerbates this problem. Therefore, it is crucial to develop effective strategies to mitigate the effects of salinity on agriculture.

Plants experience various detrimental effects from saline environments, including damage to cell membranes, increased oxidative stress, suppression of photosynthesis, osmotic stress, and imbalances in ionic concentrations. Despite these challenges, plants have evolved several mechanisms to counteract salinity. These include osmo-protection, which helps maintain cellular osmotic balance; the antioxidant defence system, which neutralizes harmful reactive oxygen species; and ionic homeostasis and compartmentalization, which manage the uptake, transport, and storage of ions to prevent toxic accumulations.

Addressing the salinity issue requires a multifaceted approach, combining insights from molecular biology, genetics, and biotechnology. Significant progress has been made in identifying genes associated with salt tolerance through techniques such as Genome-Wide Association Studies (GWAS) and transcriptome analysis. These advancements, alongside the potential applications of genetic engineering, present promising avenues for developing crops that can thrive in saline conditions. Future research should focus on the functional characterization of these candidate genes and explore multi-gene strategies to enhance salt tolerance across various plant species.

This review emphasizes the importance of ongoing research into salt tolerance genes, as they are crucial for tackling the challenges posed by saline environments on agricultural productivity. The past two decades have seen extensive research into plant responses to salinity and the mechanisms of tolerance. However, many aspects remain to be explored. Future studies should aim for a deeper understanding of the molecular and metabolic changes induced by salinity, which will be essential for developing innovative solutions to improve crop resilience and ensure sustainable agricultural practices in saline soils.

Acknowledgement

We are grateful to Dr. Neeta M. Patil, Head, Department of Botany, and Principal Dr. R. S. Zunjarrao, for providing the required research infrastructure.

Funding Sources

The author(s) received no financial support for the research, authorship, and/or publication of this article

Conflict of Interest

Authors Declare that there is no conflict of interest related with this article.

Data Availability Statement

The document used to support the review of this paper is available from the corresponding author upon reasonable request.

Informed Consent Statement

This study did not involve human participants, and therefore, informed consent was not required.

Authors' Contribution

All authors contributed equally.

References

1. Xu FJ, Jin CW, Liu WJ, Zhang YS, Lin XY. Pretreatment with H2O2 alleviates aluminum-induced oxidative stress in wheat seedlings. *Journal of Integrative Plant Biology.* 2011;53(1):44-53. doi:10.1111/j.1744-7909.2010.01008.x
2. Arora NK. Impact of climate change on agriculture production and its sustainable solutions. *Environmental Sustainability.* 2019;2(2):95-96. doi:10.1007/s42398-019-00078-w
3. Shrivastava P, Kumar R. Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi Journal of Biological Sciences.* 2015;22(2):123-131. doi:10.1016/j.sjbs.2014.12.001
4. FAO. FAOSTAT. *agricultural database http://apps.fao.org.* Published online 2015.
5. FAO. FAOSTAT. Agric database http//apps.fao.org. Published online 2009.
6. EL Sabagh A, Islam MS, Skalicky M, *et al.* Salinity Stress in Wheat (Triticum aestivum L.) in the Changing Climate: Adaptation and Management Strategies. *Frontiers in Agronomy.* 2021;3. doi:10.3389/fagro.2021.661932
7. Uçarlı C. Effects of Salinity on Seed Germination and Early Seedling Stage. In: *Abiotic Stress in Plants.* IntechOpen; 2021. doi:10.5772/intechopen.93647
8. Liang W, Ma X, Wan P, Liu L. Plant salt-tolerance mechanism: A review. *Biochemical and Biophysical Research Communications.* 2018;495(1):286-291. doi:10.1016/j.bbrc.2017.11.043
9. Munns R, Tester M. Mechanisms of salinity tolerance. *Annual Review of Plant Biology.* 2008;59:651-681. doi:10.1146/annurev.arplant.59.032607.092911
10. Safdar H, Amin A, Shafiq Y, Ali A, Yasin R. Abbas Shoukat, Maqsood Ul Hussan, Muhammad Ishtiaq Sarwar. A review: Impact of salinity on plant growth. *Nature and Science.* 2019;17(1):34-40. doi:10.7537/marsnsj170119.06
11. Parida AK, Das AB. Salt tolerance and salinity effects on plants: A review. *Ecotoxicology and Environmental Safety.* 2005;60(3):324-349. doi:10.1016/j.ecoenv.2004.06.010
12. Taiz L., Zeiger E. Plant Physiology. 2nd ed. Sinauer Associates. Inc., Publ.; 1998.
13. Qin J, Dong WY, He KN, *et al.* NaCl salinity-induced changes in water status, ion contents and photosynthetic properties of Shepherdia argentea (Pursh) Nutt. seedlings. *Plant, Soil and Environment.* 2010;56(7):325-332. doi:10.17221/209/2009-PSE
14. Sheteiwy MS, Shao H, Qi W, *et al.* Seed priming and foliar application with jasmonic acid enhance salinity stress tolerance of soybean (<scp> Glycine max L. </scp>) seedlings. *Journal of the Science of Food and Agriculture.* 2021;101(5):2027-2041. doi:10.1002/jsfa.10822
15. Hasanuzzaman M, Raihan MRH, Masud AAC, *et al.* Regulation of Reactive Oxygen Species and Antioxidant Defense in Plants under Salinity. *International Journal of Molecular Sciences.* 2021;22(17):9326. doi:10.3390/ijms22179326
16. Guo Q, Liu L, Barkla BJ. Membrane Lipid Remodeling in Response to Salinity. *International Journal of Molecular Sciences.* 2019;20(17):4264. doi:10.3390/ijms20174264
17. Amin I, Rasool S, Mir MA, Wani W, Masoodi KZ, Ahmad P. Ion homeostasis for salinity tolerance in plants: a molecular approach. *Physiologia Plantarum.* 2021;171(4):578-594. doi:10.1111/ppl.13185
18. Soliman M, Elkelish A, Souad T, Alhaithloul H, Farooq M. Brassinosteroid seed priming with nitrogen supplementation improves salt tolerance in soybean. *Physiology and Molecular Biology of Plants.* 2020;26(3):501-511. doi:10.1007/s12298-020-00765-7
19. Alves R de C, Rossatto DR, da Silva J dos S, *et al.* Seed priming with ascorbic acid enhances salt tolerance in micro-tom tomato plants by modifying the antioxidant defense system components. *Biocatalysis and Agricultural Biotechnology.* 2021;31:101927. doi:10.1016/j.bcab.2021.101927
20. Bose J, Rodrigo-Moreno A, Shabala S. ROS homeostasis in halophytes in the context

of salinity stress tolerance. *Journal of Experimental Botany.* 2014;65(5):1241-1257. doi:10.1093/jxb/ert430

21. Zamanzadeh-Nasrabadi SM, Mohammadiapanah F, Hosseini-Mazinani M, Sarikhan S. Salinity stress endurance of the plants with the aid of bacterial genes. *Frontiers in Genetics.* 2023;14. doi:10.3389/fgene.2023.1049608
22. Kim TH, Kim SM. Identification of Candidate Genes for Salt Tolerance at the Seedling Stage Using Integrated Genome-Wide Association Study and Transcriptome Analysis in Rice. *Plants.* 2023;12(6). doi:10.3390/plants12061401
23. Liu J, Xue C, Lin Y, *et al.* Genetic analysis and identification of VrFRO8, a salt tolerance-related gene in mungbean. *Gene.* 2022;836:146658. doi:10.1016/j.gene.2022.146658
24. Irshad A, Ahmed RI, Ur Rehman S, *et al.* Characterization of salt tolerant wheat genotypes by using morpho-physiological, biochemical, and molecular analysis. *Frontiers in Plant Science.* 2022;13. doi:10.3389/fpls.2022.956298
25. Qi X, Li MW, Xie M, *et al.* Identification of a novel salt tolerance gene in wild soybean by whole-genome sequencing. *Nature Communications.* 2014;5. doi:10.1038/ncomms5340
26. Wanjogu SN, Muya EM, Gicheru PT, Waruru BK. Soil degradation: Management and rehabilitation in Kenya. In: *FAO/ISCW Expert Consultation on Management of Degraded Soil in Southern and Eastern Africa (MADS-SEA) 2nd Networking Meeting.* ; 2001.
27. Cyrus DP, Martin TJ, Reavell PE. Salt-water intrusion from the Mzingazi River and its effects on adjacent swamp forest at Richards Bay, Zululand, South Africa. *Water SA.* 1997;23(1):101-108.
28. Yadav S, Irfan M, Hayat S, Aqil Ahmad. *Causes of Salinity and Plant Manifestations to Salt Stress*: A Review.; 2011. https://www.researchgate.net/publication/221818713
29. Muchate NS, Nikalje GC, Rajurkar NS, Suprasanna P, Nikam TD. Plant Salt Stress: Adaptive Responses, Tolerance Mechanism and Bioengineering for Salt Tolerance. *The Botanical Review.* 2016;82(4):371-406. doi:10.1007/s12229-016-9173-y
30. Ahmad P, Prasad MNV, eds. *Abiotic Stress Responses in Plants.* Springer New York; 2012. doi:10.1007/978-1-4614-0634-1
31. Arif Y, Singh P, Siddiqui H, Bajguz A, Hayat S. Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiology and Biochemistry*. 2020;156:64-77. doi:10.1016/j.plaphy.2020.08.042
32. Navada S, Vadstein O, Gaumet F, *et al.* Biofilms remember: Osmotic stress priming as a microbial management strategy for improving salinity acclimation in nitrifying biofilms. *Water Research.* 2020;176:115732. doi:10.1016/j.watres.2020.115732
33. Yu R, Zuo T, Diao P, *et al.* Melatonin Enhances Seed Germination and Seedling Growth of Medicago sativa Under Salinity via a Putative Melatonin Receptor MsPMTR1. *Frontiers in Plant Science.* 2021;12. doi:10.3389/fpls.2021.702875
34. Mwando E, Han Y, Angessa TT, *et al.* Genome-Wide Association Study of Salinity Tolerance During Germination in Barley (Hordeum vulgare L.). *Frontiers in Plant Science.* 2020;11. doi:10.3389/fpls.2020.00118
35. Wu L, Huo W, Yao D, Li M. Effects of solid matrix priming (SMP) and salt stress on broccoli and cauliflower seed germination and early seedling growth. *Scientia Horticulturae.* 2019;255:161-168. doi:10.1016/j.scienta.2019.05.007
36. El-Hendawy S, Elshafei A, Al-Suhaibani N, *et al.* Assessment of the salt tolerance of wheat genotypes during the germination stage based on germination ability parameters and associated SSR markers. *Journal of Plant Interactions.* 2019;14(1):151-163. doi:10.1080/17429145.2019.1603406
37. Ibrahim EA. Seed priming to alleviate salinity stress in germinating seeds. *Journal of Plant Physiology.* 2016;192:38-46. doi:10.1016/j.jplph.2015.12.011
38. Shelke DB, Pandey M, Nikalje GC, Zaware BN, Suprasanna P, Nikam TD. Salt responsive physiological, photosynthetic and biochemical attributes at early seedling stage for screening soybean genotypes. *Plant Physiology and Biochemistry.* 2017;118:519-528. doi:10.1016/j.plaphy.2017.07.013

39. Sahin U, Ekinci M, Ors S, Turan M, Yildiz S, Yildirim E. Effects of individual and combined effects of salinity and drought on physiological, nutritional and biochemical properties of cabbage (Brassica oleracea var. capitata). *Scientia Horticulturae.* 2018;240:196-204. doi:10.1016/j.scienta.2018.06.016
40. Shahzad B, Fahad S, Tanveer M, Saud S, Khan IA. Plant Responses and Tolerance to Salt Stress. In: *Approaches for Enhancing Abiotic Stress Tolerance in Plants.* CRC Press; 2019:61-78. doi:10.1201/9781351104722-3
41. Kumar S, Li G, Yang J, *et al.* Effect of Salt Stress on Growth, Physiological Parameters, and Ionic Concentration of Water Dropwort (Oenanthe javanica) Cultivars. *Frontiers in Plant Science.* 2021;12. doi:10.3389/fpls.2021.660409
42. Zörb C, Geilfus C -M., Dietz K -J. Salinity and crop yield. *Plant Biology.* 2019;21(S1):31-38. doi:10.1111/plb.12884
43. Panta S, Flowers T, Lane P, Doyle R, Haros G, Shabala S. Halophyte agriculture: Success stories. *Environmental and Experimental Botany.* 2014;107:71-83. doi:10.1016/j.envexpbot.2014.05.006
44. Maas E V., Hoffman GJ. Crop salt tolerance—current assessment. *Journal of the irrigation and drainage division.* 1977;103(2):115-134.
45. Qadir M, Quillérou E, Nangia V, *et al.* Economics of salt-induced land degradation and restoration. *Natural Resources Forum.* 2014;38(4):282-295. doi:10.1111/1477-8947.12054
46. Satir O, Berberoglu S. Crop yield prediction under soil salinity using satellite derived vegetation indices. *Field Crops Research.* 2016;192:134-143. doi:10.1016/j.fcr.2016.04.028
47. Ahmed S. Effect of soil salinity on the yield and yield components of mungbean. *Pakistan Journal of Botany.* 2009;41(1).
48. Ahmed Kalhoro N, Rajpar I, Ali Kalhoro S, *et al.* Effect of Salts Stress on the Growth and Yield of Wheat (&lt;i&gt;Triticum aestivum&lt;/i&gt; L.). *American Journal of Plant Sciences.* 2016;07(15):2257-2271. doi:10.4236/ajps.2016.715199
49. Li W. Effect of Environmental Salt Stress on Plants and the Molecular Mechanism of Salt Stress Tolerance. *International Journal of Environmental Sciences & Natural Resources.* 2017;7(3). doi:10.19080/IJESNR.2017.07.555714
50. Shah S. Morphological, Anatomical and Physiological Responses of Plants to Salinity. [*Internet*]. Published online 2014.
51. Shu S, Guo S, Sun J, Yuan L. Effects of salt stress on the structure and function of the photosynthetic apparatus in *Cucumis sativus* and its protection by exogenous putrescine. *Physiologia Plantarum.* 2012;146(3):285-296. doi:10.1111/j.1399-3054.2012.01623.x
52. Kocks P, Ross J, Bjoerkman O. Thermodynamic Efficiency and Resonance of Photosynthesis in a C3 Plant. *The Journal of Physical Chemistry.* 1995;99(44):16483-16489. doi:10.1021/j100044a043
53. Shah S, Houborg R, McCabe M. Response of Chlorophyll, Carotenoid and SPAD-502 Measurement to Salinity and Nutrient Stress in Wheat (Triticum aestivum L.). *Agronomy.* 2017;7(3):61. doi:10.3390/agronomy7030061
54. Holt NE, Zigmantas D, Valkunas L, Li XP, Niyogi KK, Fleming GR. Carotenoid Cation Formation and the Regulation of Photosynthetic Light Harvesting. *Science.* 2005;307(5708):433-436. doi:10.1126/science.1105833
55. Zakar T, Laczko-Dobos H, Toth TN, Gombos Z. Carotenoids Assist in Cyanobacterial Photosystem II Assembly and Function. *Frontiers in Plant Science.* 2016;7. doi:10.3389/fpls.2016.00295
56. Santabarbara S, Casazza AP, Ali K, *et al.* The Requirement for Carotenoids in the Assembly and Function of the Photosynthetic Complexes in *Chlamydomonas reinhardtii. Plant Physiology.* 2012;161(1):535-546. doi:10.1104/pp.112.205260
57. Najar R, Aydi S, Sassi-Aydi S, Zarai A, Abdelly C. Effect of salt stress on photosynthesis and chlorophyll fluorescence in *Medicago truncatula. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology.* 2019;153(1):88-97. doi:10.1080/11263504.2018.1461701
58. Hamani AKM, Wang G, Soothar MK, *et al.* Responses of leaf gas exchange attributes, photosynthetic pigments and antioxidant

enzymes in NaCl-stressed cotton (Gossypium hirsutum L.) seedlings to exogenous glycine betaine and salicylic acid. *BMC Plant Biology.* 2020;20(1):434. doi:10.1186/s12870-020-02624-9

59. Alasvandyari F, Mahdavi B. Effect of glycine betaine and salinity on photosynthetic pigments and ion concentration of safflower. *Desert.* 2018;23(2):265-271.
60. Kim YH, Khan AL, Waqas M, Lee IJ. Silicon Regulates Antioxidant Activities of Crop Plants under Abiotic-Induced Oxidative Stress: A Review. *Frontiers in Plant Science.* 2017;8. doi:10.3389/fpls.2017.00510
61. AbdElgawad H, Zinta G, Hegab MM, Pandey R, Asard H, Abuelsoud W. High Salinity Induces Different Oxidative Stress and Antioxidant Responses in Maize Seedlings Organs. *Frontiers in Plant Science.* 2016;7. doi:10.3389/fpls.2016.00276
62. Hussain S, Khan F, Cao W, Wu L, Geng M. Seed Priming Alters the Production and Detoxification of Reactive Oxygen Intermediates in Rice Seedlings Grown under Sub-optimal Temperature and Nutrient Supply. *Frontiers in Plant Science.* 2016;7. doi:10.3389/fpls.2016.00439
63. Hasanuzzaman M, Bhuyan MHM, Zulfiqar F, *et al.* Reactive Oxygen Species and Antioxidant Defense in Plants under Abiotic Stress: Revisiting the Crucial Role of a Universal Defense Regulator. *Antioxidants.* 2020;9(8):681. doi:10.3390/antiox9080681
64. Moradbeygi H, Jamei R, Heidari R, Darvishzadeh R. Investigating the enzymatic and non-enzymatic antioxidant defense by applying iron oxide nanoparticles in Dracocephalum moldavica L. plant under salinity stress. *Scientia Horticulturae.* 2020;272:109537. doi:10.1016/j.scienta.2020.109537
65. Ologundudu F. Antioxidant enzymes and non-enzymatic antioxidants as defense mechanism of salinity stress in cowpea (Vigna unguiculata L. Walp)—Ife brown and Ife bpc. *Bulletin of the National Research Centre.* 2021;45(1):152. doi:10.1186/s42269-021-00615-w
66. Al Kharusi L, Al Yahyai R, Yaish MW. Antioxidant Response to Salinity in Salt-Tolerant and Salt-Susceptible Cultivars of Date Palm. *Agriculture.* 2019;9(1):8. doi:10.3390/agriculture9010008
67. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry.* 2010;48(12):909-930. doi:10.1016/j.plaphy.2010.08.016
68. Ganie SA, Molla KA, Henry RJ, Bhat K V., Mondal TK. Advances in understanding salt tolerance in rice. *Theoretical and Applied Genetics*. 2019;132(4):851-870. doi:10.1007/s00122-019-03301-8
69. Momeni MM, Kalantar M, Dehghani-Zahedani M. Physiological, biochemical and molecular responses of durum wheat under salt stress. *Plant Genetic Resources: Characterization and Utilization.* 2021;19(2):93-103. doi:10.1017/S1479262120000416
70. Ahmad R, Hussain S, Anjum MA, *et al.* Oxidative Stress and Antioxidant Defense Mechanisms in Plants Under Salt Stress. In: *Plant Abiotic Stress Tolerance.* Springer International Publishing; 2019:191-205. doi:10.1007/978-3-030-06118-0_8
71. Leshem Y, Melamed-Book N, Cagnac O, *et al.* Suppression of Arabidopsis vesicle-SNARE expression inhibited fusion of H_2O_2 -containing vesicles with tonoplast and increased salt tolerance. *Proceedings of the National Academy of Sciences.* 2006;103(47):18008-18013. doi:10.1073/pnas.0604421103
72. Flowers TJ, Hajibagheri MA, Clipson NJW. Halophytes. *The Quarterly Review of Biology.* 1986;61(3):313-337. doi:10.1086/415032
73. Poljakoff-Mayber A. Morphological and Anatomical Changes in *Plants as a Response to Salinity Stress.* In: ; 1975:97-117. doi:10.1007/978-3-642-80929-3_8
74. Munns R. Comparative physiology of salt and water stress. *Plant, Cell & Environment.* 2002;25(2):239-250. doi:10.1046/j.0016-8025.2001.00808.x
75. Peng Z, He S, Sun J, *et al.* Na+ compartmentalization related to salinity stress tolerance in upland cotton (Gossypium hirsutum) seedlings. *Scientific Reports.* 2016;6(1):34548. doi:10.1038/srep34548
76. Almeida DM, Oliveira MM, Saibo NJM. Regulation of Na+ and K+ homeostasis in plants: towards improved salt stress

tolerance in crop plants. *Genetics and Molecular Biology.* 2017;40(1 suppl 1):326-345. doi:10.1590/1678-4685-gmb-2016-0106

77. Sairam RK, Tyagi A. Physiology and Molecular Biology of Stress Tolerance in Plants. Madhava Rao K., Raghavendra AS, Janardhan Reddy K, eds. *Current Science.* 2006;86(3):407-421. doi:10.1007/1-4020-4225-6
78. Wu H. Plant salt tolerance and Na+ sensing and transport. *The Crop Journal.* 2018;6(3):215-225. doi:10.1016/j.cj.2018.01.003
79. Zhang HX, Blumwald E. Transgenic salt-tolerant tomato plants accumulate salt in foliage but not in fruit. *Nature Biotechnology.* 2001;19(8):765-768. doi:10.1038/90824
80. Chen H, An R, Tang JH, *et al.* Over-expression of a vacuolar Na+/H+ antiporter gene improves salt tolerance in an upland rice. *Molecular Breeding.* 2007;19(3):215-225. doi:10.1007/s11032-006-9048-8
81. Ji H, Pardo JM, Batelli G, Van Oosten MJ, Bressan RA, Li X. The Salt Overly Sensitive (SOS) Pathway: Established and Emerging Roles. *Molecular Plant*. 2013;6(2):275-286. doi:10.1093/mp/sst017
82. Assaha DVM, Ueda A, Saneoka H, Al-Yahyai R, Yaish MW. The Role of Na+ and K+ Transporters in Salt Stress Adaptation in Glycophytes. *Frontiers in Physiology.* 2017;8. doi:10.3389/fphys.2017.00509
83. Wu GQ, Wang SM. Calcium regulates K<sup>+</sup>/Na<sup>+</sup> homeostasis in rice (Oryza sativa L.) under saline conditions. *Plant, Soil and Environment.* 2012;58(3):121-127. doi:10.17221/374/2011-PSE
84. Zhao S, Zhang Q, Liu M, Zhou H, Ma C, Wang P. Regulation of Plant Responses to Salt Stress. *International Journal of Molecular Sciences.* 2021;22(9):4609. doi:10.3390/ijms22094609
85. Nahar K, Hasanuzzaman M, Fujita M. Roles of Osmolytes in Plant Adaptation to Drought and Salinity. In: *Osmolytes and Plants Acclimation to Changing Environment: Emerging Omics Technologies.* Springer India; 2016:37-68. doi:10.1007/978-81-322-2616-1_4
86. Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany.* 2007;59(2):206-216. doi:10.1016/j.envexpbot.2005.12.006
87. Suprasanna P, Nikalje GC, Rai AN. Osmolyte Accumulation and Implications in Plant Abiotic Stress Tolerance. In: *Osmolytes and Plants Acclimation to Changing Environment: Emerging Omics Technologies.* Springer India; 2016:1-12. doi:10.1007/978-81-322-2616-1_1
88. Rösgen J. Molecular Basis of Osmolyte Effects on Protein and Metabolites. In: *Methods in Enzymology.* ; 2007:459-486. doi:10.1016/S0076-6879(07)28026-7
89. Liang X, Zhang L, Natarajan SK, Becker DF. Proline Mechanisms of Stress Survival. *Antioxidants & Redox Signaling.* 2013;19(9):998-1011. doi:10.1089/ars.2012.5074
90. Tang X, Mu X, Shao H, Wang H, Brestic M. Global plant-responding mechanisms to salt stress: physiological and molecular levels and implications in biotechnology. *Critical Reviews in Biotechnology.* 2015;35(4):425-437. doi:10.3109/07388551.2014.889080
91. Singh M, Kumar J, Singh S, Singh VP, Prasad SM. Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Reviews in Environmental Science and Bio/Technology.* 2015;14(3):407-426. doi:10.1007/s11157-015-9372-8
92. Zulfiqar F, Akram NA, Ashraf M. Osmoprotection in plants under abiotic stresses: new insights into a classical phenomenon. *Planta.* 2020;251(1):3. doi:10.1007/s00425-019-03293-1
93. Syeed S, Sehar Z, Masood A, Anjum NA, Khan NA. Control of Elevated Ion Accumulation, Oxidative Stress, and Lipid Peroxidation with Salicylic Acid-Induced Accumulation of Glycine Betaine in Salinity-Exposed Vigna radiata L. *Applied Biochemistry and Biotechnology.* 2021;193(10):3301-3320. doi:10.1007/s12010-021-03595-9
94. Rady MOA, Semida WM, Abd El-Mageed TA, Hemida KA, Rady MM. Up-regulation of antioxidative defense systems by glycine betaine foliar application in onion plants confer tolerance to salinity stress. *Scientia Horticulturae.* 2018;240:614-622.

doi:10.1016/j.scienta.2018.06.069

95. Suprasanna P, Rai AN, Kumari PH, Kumar SA, Kishor PBK. Modulation of proline: implications in plant stress tolerance and development. In: *Plant Adaptation to Environmental Change: Significance of Amino Acids and Their Derivatives.* CABI; 2014:68-96. doi:10.1079/9781780642734.0068
96. Slama I, Abdelly C, Bouchereau A, Flowers T, Savouré A. Diversity, distribution and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. *Annals of Botany.* 2015;115(3):433-447. doi:10.1093/aob/mcu239
97. Koster KL. Glass Formation and Desiccation Tolerance in Seeds. *Plant Physiology.* 1991;96(1):302-304. doi:10.1104/pp.96.1.302
98. Pukacka S, Ratajczak E, Kalemba E. Non-reducing sugar levels in beech (Fagus sylvatica) seeds as related to withstanding desiccation and storage. *Journal of Plant Physiology*. 2009;166(13):1381-1390. doi:10.1016/j.jplph.2009.02.013
99. Zhang Q, Dai W. Plant Response to Salinity Stress. In: *Stress Physiology of Woody Plants. CRC Press;* 2019:155-173. doi:10.1201/9780429190476-7
100. Saeidnejad AH, Rajaei P. Antioxidative responses to drought and salinity stress in plants, a comprehensive review. *International Journal of Life Sciences.* 2015;9(2):1-8. doi:10.3126/ijls.v9i2.12042
101. Butt M, Sattar A, Abbas T, *et al.* Morpho-physiological and biochemical attributes of Chili (Capsicum annum L.) genotypes grown under varying salinity levels. PLOS ONE. 2021;16(11):e0257893. doi:10.1371/journal.pone.0257893
102. Willekens H. Catalase is a sink for H2O2 and is indispensable for stress defence in C3 plants. *The EMBO Journal.* 1997;16(16):4806-4816. doi:10.1093/emboj/16.16.4806
103. Nefissi Ouertani R, Abid G, Karmous C, *et al.* Evaluating the contribution of osmotic and oxidative stress components on barley growth under salt stress. *AoB PLANTS*. 2021;13(4). doi:10.1093/aobpla/plab034
104. Siegel BZ. Plant peroxidases—an organismic perspective. *Plant Growth Regulation.* 1993;12(3):303-312. doi:10.1007/BF00027212
105. Asada K. Ascorbate peroxidase – a hydrogen peroxide-scavenging enzyme in plants. *Physiologia Plantarum.* 1992;85(2):235-241. doi:10.1111/j.1399-3054.1992.tb04728.x
106. Mushtaq Z, Faizan S, Gulzar B. Salt stress, its impacts on plants and the strategies plants are employing against it: A review. *Journal of Applied Biology & Biotechnology.* 2020;8(3):81-91. doi:10.7324/JABB.2020.80315
107. Hasanuzzaman M, Bhuyan MHMB, Anee TI, *et al.* Regulation of Ascorbate-Glutathione Pathway in Mitigating Oxidative Damage in Plants under Abiotic Stress. *Antioxidants.* 2019;8(9):384. doi:10.3390/antiox8090384
108. Bela K, Horváth E, Gallé Á, Szabados L, Tari I, Csiszár J. Plant glutathione peroxidases: Emerging role of the antioxidant enzymes in plant development and stress responses. *Journal of Plant Physiology.* 2015;176:192-201. doi:10.1016/j.jplph.2014.12.014
109. Nianiou-Obeidat I, Madesis P, Kissoudis C, *et al.* Plant glutathione transferase-mediated stress tolerance: functions and biotechnological applications. *Plant Cell Reports.* 2017;36(6):791-805. doi:10.1007/s00299-017-2139-7
110. Akram NA, Shafiq F, Ashraf M. Ascorbic Acid-A Potential Oxidant Scavenger and Its Role in Plant Development and Abiotic Stress Tolerance. *Frontiers in Plant Science.* 2017;8. doi:10.3389/fpls.2017.00613
111. Noreen S, Sultan M, Akhter MS, *et al.* Foliar fertigation of ascorbic acid and zinc improves growth, antioxidant enzyme activity and harvest index in barley (Hordeum vulgare L.) grown under salt stress. *Plant Physiology and Biochemistry.* 2021;158:244-254. doi:10.1016/j.plaphy.2020.11.007
112. Hasanuzzaman M, Nahar K, Anee TI, Fujita M. Glutathione in plants: biosynthesis and physiological role in environmental stress tolerance. *Physiology and Molecular Biology of Plants.* 2017;23(2):249-268. doi:10.1007/s12298-017-0422-2
113. Young AJ. The photoprotective role of carotenoids in higher plants. *Physiologia Plantarum.* 1991;83(4):702-708. doi:10.1111/j.1399-3054.1991.tb02490.x
114. Ben-Abdallah S, Zorrig W, Amyot L, *et al.* Potential production of polyphenols,

carotenoids and glycoalkaloids in Solanum villosum Mill. under salt stress. *Biologia.* 2019;74(3):309-324. doi:10.2478/s11756-018-00166-y

115. Munné-Bosch S. The role of -tocopherol in plant stress tolerance. *Journal of Plant Physiology.* 2005;162(7):743-748. doi:10.1016/j.jplph.2005.04.022
116. Yang Y, Guo Y. Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytologist. 2018;217(2):523-539. doi:10.1111/nph.14920
117. Razzaque S, Elias SM, Haque T, *et al.* Gene Expression analysis associated with salt stress in a reciprocally crossed rice population. *Scientific Reports.* 2019;9(1):8249. doi:10.1038/s41598-019-44757-4
118. Munns R. Genes and salt tolerance: Bringing them together. New *Phytologist.* 2005;167(3):645-663. doi:10.1111/j.1469-8137.2005.01487.x
119. Athar HUR, Zulfiqar F, Moosa A, *et al.* Salt stress proteins in plants: An overview. *Frontiers in Plant Science.* 2022;13. doi:10.3389/fpls.2022.999058
120. Zamanzadeh-Nasrabadi SM, Mohammadiapanah F, Hosseini-Mazinani M, Sarikhan S. Salinity stress endurance of the plants with the aid of bacterial genes. *Frontiers in Genetics.* 2023;14. doi:10.3389/fgene.2023.1049608