Plants Stress: Salt Stress and Mechanisms of Stress Tolerance

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ABSTRACT

A diverse combination of biotic and abiotic pressures makes up the environment that plants naturally inhabit. These pressures cause similarly complicated responses in plants. The purpose of the review is to critically evaluate the effects of various stress stimuli on higher plants with an emphasis on the typical and distinctive dose-dependent responses that are essential for plant growth and development. In order to improve agricultural productivity, breed new salt-tolerant cultivars, and make the most of saline land, it is essential to comprehend the mechanisms underlying plant salt tolerance. Soil salinization has emerged as a global problem. Locating regulatory centres in complex networks is made possible by systems biology techniques, enabling a multi-targeted approach. The goal of systems biology is to organise the molecular constituents of an organism (transcripts, proteins, and metabolites) into functioning networks or models that describe and forecast the dynamic behaviours of that organism in diverse contexts. This review focuses on the molecular, physiological, and pharmacological mechanisms that underlie how stress affects genomic instability, including DNA damage. Additionally, a summary of the physiological mechanisms behind salt tolerance, including the removal of reactive oxygen species (ROS) and osmotic adjustment, has been provided. The salt overly sensitive (SOS), calcium-dependent protein kinase (CDPK), mitogen-activated protein kinase (MAPKs), and abscisic acid (ABA) pathways are the four main signalling pathways for stress. According to earlier research, salt stress causes harm to plants by inhibiting photosynthesis, upsetting ion homeostasis, and peroxiding membranes. listed a few genes that are sensitive to salt stress and correspond to physiological systems. The review describes the most recent tactics and procedures for boosting salt tolerance in plants. We can make predictions about how plants will behave in the field and better understand how they respond to different levels of stress by understanding both the positive and negative aspects of stress responses, including genomic instability. The new knowledge can be put to use to enhance crop productivity and develop more resilient plant kinds, ensuring a consistent supply of food for the global population, which is currently undergoing rapid expansion.

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Introduction

The effects of biotic stress on the development and growth of plants can include reduced biomass, disruption of photosynthesis, and altered morphology. Usually, this causes the manufacture of defensive compounds such phenolics and alkaloids, which can reduce the nutritional value of crops. A plant's response to biotic stress is influenced by the type of stress, its severity, and how well the plant can deploy its defensive mechanisms.[1] A number of hormonal pathways are activated by plants in response to biotic stress.[1, 2]

The Jasmonic acid (JA) pathway is essential for plant defence against necrotrophic fungi, certain bacterial diseases, and insect herbivores. In response to these stresses, plants release jasmonic acid (JA), which kicks off a sequence of signalling events that eventually activate defence-related genes and result in the production of specialist metabolites such phytoalexins and protease inhibitors.[3] Another important phytohormone, salicylic acid (SA), is essential for plants' defence against biotic stress. It causes the expression of genes that produce proteins related to pathogenesis that directly combat the disease or stop it from spreading.[4, 5] Moreover, giving exogenous SA therapy can strengthen the host defence system. A variety of biotic stresses, including pathogen infection, mechanical injury, and insect herbivory, also cause the ethylene pathway to becoming active. As a result, ethylene levels rise, defence-related proteins and secondary metabolites are produced, and defence-related signalling pathways are activated. The aforementioned regulatory mechanisms, which are involved in plant defence, differ noticeably from one another but also come together to provide pathogen defence. Moreover, phytohormones such as auxin, brassinosteroids, cytokinin, gibberellins, and peptide hormones as well as abscisic acid (ABA), gibberellins, and auxin are involved in controlling plant immunological responses.[6, 7, 8] Among these, JA plays a crucial role in activating the plant defence mechanism and interacts with other phytohormonal pathways.

Abiotic stressors (UV) include, but are not limited to, water stress, temperature variations, uneven food and mineral levels, exposure to various types of radiation, such as ionising radiation (IR) & non-ionizing and high and low linear energy transfer (LET), as well as ultraviolet radiation.

One of the most pressing environmental problems of the twenty-first century is soil salinity. Since there is an increasing number of people to feed and not sufficient agricultural land to plant on, it is vital to find a solution to the soil salinity problem. We currently only have two main methods for reducing soil salinization: utilising chemical additives to repair soil degradation and applying biotechnology to grow salt-tolerant plant varieties. When comparing the two, the former method is seen to be expensive and runs the danger of creating secondary salinization. As a result, growing plants that can withstand salt is crucial and calls for increased effort.

Almost all of the crops that people may consume are glycophytes, and they're sensitive to soils with high salt content. However, alternative plants, referred to as halophytes, have been engineered to be salt-tolerant.[9] Researchers have been studying salt mechanisms for tolerance in salt-tolerant plants in order to apply similar processes for plants that aren't salt-tolerant. In earlier studies, a sizable chunk of the overall defence network was located.

Salt stress consists of two factors. Short-term salt stress led to osmotic stress, but accumulation of phytotoxic ions, particularly Na+ and Cl, led to long-term ion toxicity. Along with its poisonous and osmotic effects, salt stress also leads to oxidative stress, which furthers the negative effects of salinity on plants.[10]

Climate change is a complicated process that affects a wide range of plants as well as their habitats and ecosystems because of altered weather patterns and an increase in the frequency of catastrophic weather events. Also, it helps illnesses and pests spread. To endure environmental obstacles and ensure their survival against diverse threats, plants have evolved complex defence mechanisms. A potential tactic for mitigating the effects of climate change is to modify the structural elements of plants to alter their anatomy and morphology.[11] Plants have evolved ways to repair or tolerate DNA damage at the genetic level, enabling them to preserve the integrity of their genomes. The stability of the plant genome is examined in a recent review by Hartmann,[9]

which tracks the effects of various stresses while highlighting the essential underlying mechanisms. They suggest that stress-related environmental changes, such as gene expression changes, mutations, and epigenetic modifications, can affect plant DNA. The growth, development, and capacity of plants to respond to changing environmental factors can all be significantly impacted by these changes. It has been emphasized how important it is to understand how genetic and epigenetic factors may interact to determine how plants respond to stress (Fig. 1).
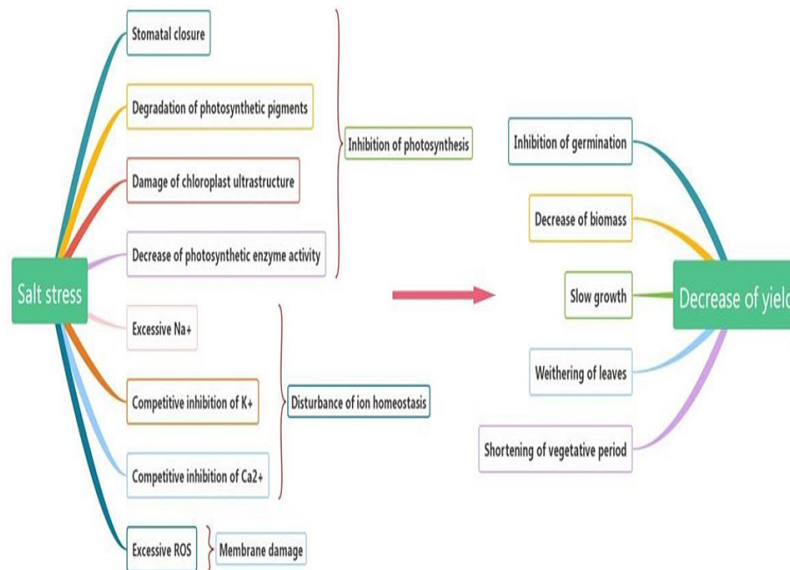

Fig. 1: Stress Response

Plants' Responses to Heat and Salt Stress

According to earlier studies by Kaplan, F., *et al.*,[12] plants under salt stress exhibit indications of delayed growth, decreased plant height, reduced growth of new branches, a lower germination rate, and wilted leaves. Denaturation of proteins and membrane instability, among other changes brought on by extreme temperatures in plants, lead to redox tension and an accumulation of ROS. The onset of heat stress can also be influenced by radiation exposure. Osmotic and ionic stress is brought on by salt stress, which is brought on by highly salinized soil. The ensuing osmotic stress sometimes referred to as dehydration stress, causes a drop in the water content of the plant. Droughts are the main cause of dehydration stress, but cold, frost, heat, and salt can all cause it as secondary stress. Moreover, it happens as a secondary stress after radiation stress.[12] By altering K+/Na+ balance, ionic stress can alter plant metabolism, interfere with membrane construction, and alter enzyme performance. These changes could result in oxidative stress becoming more pronounced as a subsequent stressor, a rise in ROS levels, and nutritional problems.[13, 14] Plants respond metabolically similarly to salt stress and drought via two separate processes, salt stress produces these outcomes.[15]

First, salt stress, also known as osmotic stress, causes plants to absorb less water, which inhibits plant growth. Then, if there are too many salty ions in the transpiration stream of the plant, they will damage the plant cells by obstructing photosynthesis, impairing ion a state of equilibrium and oxidising lipids in the membranes, further stunting plant growth and resulting in ion toxicity. Boosting plant salt tolerance requires an understanding of the physiological processes by that plants react to salt stress.

Researchers found through these analyses that being subjected to particle energy and low-energy ions that are heavy in the shoot apical meristem, embryos or intact seeds results in post-embryonic developmental defects in *Arabidopsis thaliana*. In addition, several researchers hypothesised that

this phenomenon might result from ROS activating auxin-dependent transcription mechanisms as well as a rise in homologous recombination events brought on by the induction of long-distance DNA damage.[16, 17, 18] These results have been confirmed by study on *Medicago truncatula*, which examines bystander impacts.[19] Changes in hormone levels, histone modification, and DNA methylation patterns have been discovered as a result of a thorough examination of the mechanisms underlying bystander effects.[20] Chromosome damage has been linked to micronuclei, rearrangements, sister chromatid exchanges (SCEs), altered gene expression, mutations, cell death, differentiation, and changes in microRNA (miRNA) profiles.[21]

It has been demonstrated that bystander effects result from plant communication when UV-C and X-ray radiation are applied to *Arabidopsis* plants kept in petri dishes. Similar reactions have been associated with a variety of biotic stresses, including infection by pathogens and infestation by pests, as well as abiotic stressors. Following infection with the tobacco mosaic virus in one tobacco plant, both a susceptible and a resistant cultivar experienced an increase in numbers of homologous recombination activities that spread to unaffected tissue. Other bystander-like effects in plant-to-plant interactions have been observed when volatile organic compounds produced by cabbage plants harmed by herbivores stimulate nearby, uninjured plants to produce defensive traits.[22]

Reduction in Photosynthesis

Photosynthesis is the primary generator of the nutrients and energy needed for the development and growth of plants. The rate of photosynthetic activity, water potential, leaf temperature, transpiration rate, osmotic potential, and relative water content of plant leaves are all significantly impacted by salt stress, according to studies. The components of photosynthetic structures, such as photosynthetic pigments, membrane lipids, thylakoid membrane proteins, and enzymes, are similarly affected by salt stress. Photosynthesis is negatively impacted by salt stress in two ways. First of all, plants' close stomata, when they are under salt stress, which lowers the level of CO_2 inside their cells. Second, salt stress results in various limitations unrelated to the stoma, including damage to the photosynthetic membrane system, decreased CO_2 absorption capability, impaired photosynthetic pigments, and others.

Stomata, composed of guard cells, are specialised epidermal cells that produce pores on the surface of plant leaves. The transport of H_2O during transpiration and the absorption of CO_2 during photosynthesis are both regulated by stomatal movement. Mature guard cells lacking plasmodesmata, possess thickened cell walls, and are organised in a radial pattern, allowing them to respond to changes in turgor pressure and regulate stomatal opening. When the osmotic pressure within the cells falls, the contraction of guard cells increase and water outflow will result the stoma closure. Salt stress typically causes leaves to have higher Na^+ and Cl^- levels, which lowers their K^+ content and finally leads to stoma closure. Reduced stoma opening substantially impedes CO_2 transfer from the environment to the chloroplast, which reduces intercellular CO_2 concentration and the activity of photosynthesis.

In addition to limiting stomatal openings, salt stress negatively impacts several other aspects of photosynthesis without affecting the stoma. Salt stress frequently causes chlorophyll, the most significant pigment involved in photosynthesis in salt-sensitive plants, to decrease. The leaves of hybrid *Pennisetum* had an 11.4–31.5% decrease in leaf pigment content as a result of short-term drought, long-term mild salinity, and the combination of these stressors. Comparable effects of salt stress on chlorophyll levels were seen in rice, soybeans, and pepper. The ultrastructure of chloroplasts is similarly impacted by salt stress. The most significant chloroplast structure, the thylakoid membrane, is where the light reaction takes place. Salt stress affects plants in some ways, including causing the granum connection to become loose, enlarging the cavity in the thylakoid, damaging the chloroplast bilayer, and increasing the number of lipid globules occurred in most higher plants like *Sulla coronaria, Thellungiella salsuginea*, and *Cucumis sativus*.[23]

Additionally, salt stress affects molecules related to photosynthesis, in particular enzymes and structural proteins involved in photosynthetic electron transport, light energy absorption, and CO_2 fixation. A connection between the photosynthetic process and glucose-6-phosphate dehydrogenase (G6PDH).

They suggested that under salt stress, it could offer NADPH to regulate passing electron flow around the PSI in Physcomitrella patens. By interfering with the oxygen-evolving complex's ability to operate, impeding electron transfer from Plastoquinone A (QA) to Plastoquinone B (QB), and interfering with the function of the pigment-protein complex on the thylakoid membrane, salt stress decreases the efficiency of electron transfer. Rubisco, a rate-limiting enzyme in photosynthesis, is impacted by salt stress as well. Salt stress inhibits Rubisco activity and restricts ribulose-1, 5-bisphosphate (RuBP) regeneration, which affects plant absorption and CO_2 uptake. According to research, salt stress results in stomatal restrictions and non-stomatal limits, which prevent plants that can withstand salt from growing by inhibiting photosynthesis. The aforementioned viewpoints aren't held by everyone, though. Although there have been numerous observations on how salt stress affects plant photosynthesis, no clear consensus has yet been reached. Some people think that stomatal closure results from the physiological drought brought on by salt stress. The decline in plant water potential under salt stress, according to some studies, does not occur simultaneously with the decline in photosynthetic rate. It's a common misconception that a decrease in leaf water potential causes stomatal closure. According to others, the feedback effect that happens when plants grow in salty soils restricts photosynthesis by raising the level of sugar in storage tissues. However, this perspective cannot account for the extremely low glucose concentration found in the stems of perennial woody species that have been exposed to protracted salt stress. As a result, additional study is needed to determine how photosynthesis works in plants to lessen salt stress.

Changes in Ion Homeostasis

Mineral elements, which normally reside as ions in plant cells, make up the structural elements of cells. Mineral substances function as a coenzyme and enzyme components to control enzyme activity. They also participate in the electrochemical processes of colloidal stabilisation, osmotic regulation, and charge neutralisation. The harmony of ion metabolism is necessary for the proper functioning and stability of the cell membrane and the support of the development and growth of plants. An excessive concentration of Na+ and Cl- and a corresponding deficiency of other vital ions, most notably Ca2+ and K+, are the principal causes of salt damage. Because there is so much Na+ in the soil, it accumulates in plants. Lowered membrane potential and promoted Cl uptake along a chemical gradient are both effects of high Na+ concentrations. Several enzymes and cell metabolism are harmed by too much Na+. A high Na+ concentration impairs cell division and development by causing an osmotic imbalance, membrane malfunction, and an increase in ROS generation. In addition to impeding plant growth, a high concentration of Cl lowers the amount of chlorophyll and damages the organelle and cell membrane structure. In addition to its toxic effects, Na+ clearly competes with K+ due to its similar hydration energy and ionic radius of K+. The majority of cells keep the cytoplasmic concentrations of K+ and Na+ at relatively high and low, respectively, levels to ensure their biological function. Therefore, a considerable external Na+ input will prevent K+ inflow, which causes plant damage due to K+ insufficiency. Na+ is a critical element engaged in signal transduction of several physiological processes in plants, and as a result of Na+'s competitive inhibition, the Ca2+ level in cells also falls. The Ca2+/Na+ ratio in *Schizonepeta tenuifolia* blossoms reduced as a result of growing NaCl content. Another method of regulating the osmotic stress of plants under excessive Na+ concentrations is the compensatory drop in Ca2+. Moreover, the recent experiment showed that plants' ability to absorb NH4+ and NO3 will be hindered in a salt-stressed environment. In a nutshell, salt stress disrupts the ion balance in the cells of plants, which affects plant growth and development.[24]

Membrane Injury

As a crucial protective barrier for plant cells, the cell membrane is crucial for the movement of substances, the transmission of energy, and the transmission of signals. The cell membrane's ability to selectively permeate allows it to control ion homeostasis and maintain plant physiological functions. However, increased ROS production under salt stress causes the membrane to become significantly more permeable and less fluid, which causes catastrophic damage. On the one hand, it affects the transit, selectivity, and flow rate of the ions. On the other hand, it also leads to the exosomes transport of a sizable number of electrolytes, which results in osmotic stress. Membrane-bound proteins and enzymes may

become inactive as a result of MDA, one of the main by-products of membrane lipid peroxidation. The MDA concentration serves as a critical determinant of the degree of plasma membrane damage. According to latest studies, *Carex rigescens* had a markedly higher MDA concentration following salt stress.[25] During salt stress, the MDA concentration in soybean manifested a clear increase.[26] Moreover, an increase in ROS can damage the organelle structures within cells, including the endoplasmic reticulum's growth and the membrane of the vacuole. In other words, oxidative stress, which hinders plant growth and development, is caused by excessive ROS generation in plant cells as a result of salt stress.

The reduction in protein synthesis rate is caused by the breakdown of plant cell structure, the build-up of ROS, and the disruption of ion homeostasis. The build-up of amino acids results in the formation of numerous harmful chemicals since the body is unable to synthesis protein. For instance, a lot of nitrogen metabolism's intermediates, such as NH3 and several free occurring amino acids (like ornithine, isoleucine, and arginine), are changed into some hazardous polyamines (e.g., glutamine, butane diamine, etc.). These harmful polyamines, particularly putrescine, are subsequently oxidised to form H2O2 and NH3. Plants may suffer if the concentration of such harmful compounds rises above a particular point. In conclusion, the build-up of these compounds will prevent plants from synthesising several crucial molecules, which will restrict plant growth.

Salt Stress Signs in Plants

Discussing of morphological indicators, it is normal practise to consider the weight of the shoot, root, and leaves, the length of the roots and shoots, and the shoot's width when evaluating salt stress. The growth of plants under salt stress can be accurately represented by an indicator called biomass. During salt stress, plant biomass generally declines, but the rate of decline varies amongst plants. A 50 mM NaCl spray reduced the biomass in tomato and sunflower, whereas a 100–150 mM NaCl application reduced the biomass in wheat, rice, and maize [9]. Halophytes like Salicornia do not see a drop in biomass until the NaCl concentration is 400 mM or higher. Th e evaluation of Na+ or Cl concentration in the roots and leaves is the first physiological indicator of salinity

stress in plants. Both K+ content and K+/Na+ ratio is frequently utilised. After being treated with 100 mM NaCl for 4 hours, *Arabidopsis*' K+ level decreased. Moreover, because they affect nutrient intake, ratios of other ions including Na+/Ca2+, Ca2+/Mg2+, and Cl/NO3 are frequently assessed. Moreover, the photosynthetic process is slowed down by salinity stress. Stomatal conductance, chlorophyll fluorescence, and chlorophyll concentrations are also measured under salt stress. A 100 mM concentration of 3D salt reduced the chlorophyll content of *Triticum aestivum*.[27] Salt stress and osmotic stress frequently interact. Typically, this is determined by osmotic pressure, relative water content (RWC), turgor pressure, and water potential changes. For instance, tomatoes lose some of their water potential after receiving exposure to 100 mM NaCl for two hours. When maize is exposed to 60 mM NaCl for 7 days, RWC declines. When exposed to salt stress, the ROS is greatly elevated. Typically, a rise in ROS production under salt stress damages cell membranes. Thus, leakage of electrolytes and water loss are indicators of cell membrane breakdown, which is another symptom of salt stress. As an illustration, the loss of electrolytes in sunflowers increases two days after 100 mM NaCl treatment. Additionally, signs of lipid peroxidation such as MDA levels increase during salinity stress. The thermal imaging and the hyperspectral reflectance method can also be used to evaluate the instability of the membranes by looking at how well plants reflect and absorb light at different wavelengths.

Transcriptome investigation of plants under salt stress revealed that some genes' expression altered in response to various salt concentrations. Plant salt stress can be predicted and confirmed using these genes as molecular indicators. Molecular indicators for stress assessment are rarely used in practical research compared to morphological and physiological examinations which are less expensive and easier to conduct. Despite the fact that many morphological and physiological markers, such as RWC, MDA concentration, and chlorophyll content, are activated by salt stress as well as other stresses, many morphological markers, such as plant shoot height and diameter, are only visible after the plant has already sustained significant damage. On the other hand, molecular indicators could be able to predict the level of salt stress earlier and more precisely. Yet, any stress indicator has its limitations,

whether they are morphological, physiological, or molecular changes in plants. Further research is needed to integrate morphological, physiological, and molecular methods for detecting plant stress.

Physiological Mechanisms of Salt Stress Tolerance

Increasing plant tolerance to salt stress or lowering the concentration of salty ions are the two ways to diminish the harm that salt stress causes to plants. There are four ways in which plants might defend themselves against salt damage: salt dilution, salt build-up, salt excretion, and salt exclusion. Salt excretion, which is common in halophytes, is the mechanism by which plants sustain equilibrium between ions by excreting surplus salt from their salt glands. Plants use a technique known as salt dilution to reduce the quantity of salt in their bodies by absorbing huge amounts of water or by enlarging their cell size. Plants use salt build-up as a mechanism to store extra salt in vacuoles and lessen the damage it causes to other cell components. With the help of some unique structures, plants use the tactic of salt exclusion to keep salt from ingesting their bodies. In addition to the four strategies listed above, each of the higher plants can increase their tolerance to salt stress by utilising the ROS scavenging physiological regulation and osmotic adjustment processes.

Natural Ions

In dicotyledons, 80% to 95% of the cell's osmotic pressure is made up of inorganic ions, primarily K, Na, and Cl. K+ is a crucial component for plant growth and is crucial in preventing salt stress-related damage to plant cells. Chakraborty demonstrated that exogenous K+ treatment altered the hydration state of plants to increase biomass and enhance salt tolerance under stress in peanuts.[28] Halophytes absorb Na+ far more easily than K+. The majority of the Na+ absorbed by plant cells is not located in the cytoplasm but is instead confined in vacuoles, where it acts as an osmotic controller to sustain cell turgor pressure. For example, seedlings of two varieties of cabbage, one salt-sensitive and the other salt-tolerant, were each given NaCl treatment for 30 days. The findings showed that the main method of salt adaptation in Chinese cabbage was to separate Na+ into vacuoles. Regarding Cl, fast Cl uptake by plants during the early stages of salt stress encouraged non-halophytes to regulate their root

systems through osmotic pressure. Cl still needs Na+ or K+ to complete the osmotic pressure regulation, though. Ca2+ content in the cytoplasm is essential for signal transduction. When plants experience salt stress, Ca2+ channels are encouraged to open. Ca2+ is then released by the vacuole. When calcium interaction with calcic binding proteins or calmodulin, regulates cell metabolism and gene expression, plants are better able to respond to adversity. To put it another way, plants maintain their ability to absorb water from the soil when they are exposed to salt stress by increasing the ratio of inorganic ions like K+ and organic molecules like proline and betaine.

ROS Scavenging

During the metabolic process, oxygen will be transformed into non-radical ROS and free radical ROS. Superoxide radical (O2), alkoxyl radical (RO) and hydroxyl radical (OH) are typical examples of free radicals, while hydrogen peroxide (H2O2) and singlet oxygen are typical examples of non-radicals. The production of ROS is reported to occur naturally in plants as a by-product of aerobic metabolism. Under typical circumstances, the antioxidant defence system in plants maintains a balance between the generation and scavenging of ROS. In addition, ROS are signals that control many critical biological processes. They can specifically be employed as molecules that signal harm to help plants react to stress. Yet, in a stressful environment, excessive ROS production upsets the balance between ROS build-up and scavenging, leading to oxidative cell damage.[29] Given their lengthy evolutionary history, plants have built up a complex network of antioxidant defences to cut down on ROS overproduction in response to various abiotic challenges. The antioxidant defence system consists of two different types of antioxidants, namely enzymatic antioxidants (superoxide dismutase, SOD; catalase, CAT; peroxidases, POD; ascorbate peroxidase, APX; monodehydroascorbate reductase, MDHAR; dehydro-ascorbate reductase, DHAR; glutathione reductase, GR; glutathione peroxidase, GPX; &glutathione S-transferase, GST) and non-enzymatic antioxidants (ascorbic acid, AsA; glutathione, GSH; carotenoids, CAR; α-tocopherol; &some alkaloids as well as some flavonoids).

Enzymatic Antioxidants

SOD serves as the initial line of defence against oxidative stress in plants' entire antioxidant

enzymatic system. It transforms O_2 into H_2O_2. SOD can be divided into Fe-SODs, Mn-SODs, and CuZn-SODs based on the variations in the metal ions that bind to the SOD. Fe-SODs, CuZn-SODs and Mn-SODs are primarily found in chloroplasts, mitochondria, and extracellular space, respectively. A salt-sensitive sweet potato was given CuZnSOD therapy utilising the stress-inducible SWPA2 promoter.[30] During salt stress, the transgenic plants' expression levels were found to be significantly higher than those of the natural type. PhOH, a phenolic molecule, is oxidised by POD to create PhO, a phenoxyl radical. H_2O_2, which serves as an electron acceptor in this reaction, is transformed into $2H_2O$. POD is abundantly present in tissues of many plants. As an adaptable enzyme with high activity, it can reflect characteristics of growth of plant and development, metabolism condition in vivo, and environmental adaptability. POD activity was found to have risen in the tests with the aid of arbuscular mycorrhizal fungus (AMF) in response to the ROS damage under NaCl treatment. CAT may break down H_2O_2 quickly, releasing H_2O and O_2. The potential of CAT to reduce oxidative damage is demonstrated by the fact that in plants, the higher the CAT activity, the smaller the rising ratio of H_2O_2 is. There are three CAT isoenzymes: CAT1, CAT2, and CAT3. These enzymes are mainly found in peroxisomes and glyoxysomes. When ROS scavenging in plants was explored in relation to the effect of H_2O_2 pre-treatment on maize leaves, CAT initially showed the strongest response to H_2O_2 and the highest degree of activity.[31] (Fig. 2).
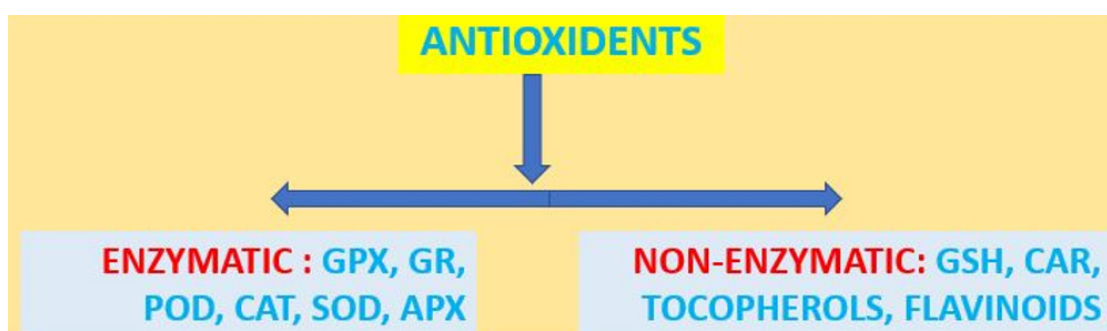

Fig. 2: Stress Tolerence Factors

H_2O_2 can be used as an oxidant in APX to catalyse the conversion of AsA to MDHA. Higher plants' APX isoenzymes are divided into two groups: cytosolic APX (cAPX) and chloroplast APX (chlAPX). The thylakoid-bound APX and stroma APX (sAPX) are two types of chloroplasts APX (tAPX). The cytoplasmic types include isoenzymes that are located in microsomes (peroxisomes, glyoxysomes), as well as some whose cytoplasmic location is still unknown. The oxidation of AsA to form DHA and subsequently MDHA, as well as the detoxification of H_2O_2, is processed in which all isoenzymes can take part. Transgenics overexpressing cytosolic ascorbate peroxidase (RaAPX), cytosolic CuZn-superoxide dismutase (PaSOD), and dual transgenics overexpressing both the genes in *Arabidopsis thaliana* changed the expression of genes involved in the response to salt stress and the formation of secondary cell wall cellulose.[32] Additional enzymes play a role in the AsA-GSH cycle's regeneration of GSH and AsA but do not directly interact with ROS. An enzyme called MDHAR, which is dependent on NADH or NADPH, is used to regenerate AsA from MDHA. In order to achieve AsA regeneration, DHAR catalyses the process of oxidation of DHA. Another crucial enzyme in the AsA-GSH cycle, GR converts GSSG to GSH to control redox equilibrium.[33] Enzyme GPX may decrease H_2O_2 and shield cells from damage caused by oxidation with the aid of GST by using GSH and thioredoxin. Recent investigation yielded convincing evidence that the AsA-GSH cycle plays a role in the Egyptian lentil cultivars' (Lens culinaris) mechanism for salt tolerance.

Non-Enzymatic Antioxidants
Active growth regions like meristems, photosynthetic cells, root tips, flowers, and immature fruits are rich in AsA, a potent water-soluble antioxidant. Usually, by functioning as a co-enzyme and supplying

electrons, AsA plays a significant part in scavenging ROS while under stress. Moreover, AsA takes part in the regeneration of the significant antioxidant α-tocopherol. AsA is also believed to be essential for the functioning of the photosynthetic system, the mitochondrial oxidative phosphorylation system, and the control of the cellular redox state. Exogenous AsA has been shown in numerous studies to boost plant resilience to salt stress and promote plant development. For example, exogenous AsA significantly accelerated the development of wheat seedlings under water stress. Oxidised glutathione (GSSG) and reduced glutathione (GSH) can be converted into one another by plants. GSH plays a crucial role in managing intracellular defence by scavenging ROS. Moreover, as a part of the AsA-GSH cycle, GSH preserves redox equilibrium. H_2O_2 is reduced to water by APX in the first phase of the AsA-GSH cycle, which uses AsA as the electron donor. The MDHAR regenerates the oxidised AsA (MDHA). Nevertheless, MDHA is a free radical and will convert to DHA if it is not quickly decreased. DHAR converts DHA to AsA at the expense of GSH, resulting in GSSG. Finally, GR converts GSSG to GSH by using NADPH as an electron donor. GSH and AsA are not depleted as a result. Exogenous GSH and AsA increased the levels of endogenous GSH and AsA, decreased the levels of H_2O_2 and MDA, and boosted the activities of APX, GR, and SOD in the chloroplasts of two Oryza sativa varieties under salt stress.[34] These results suggest that exogenous GSH and AsA may be beneficial for ROS scavenging and salt stress resistance. Chloroplasts can use CAR as additional pigments for light absorption. Additionally, it can remove ROS produced by photosynthetic machinery. CAR protects the photosystem in four different ways: they engage in interactions with lipid peroxidation products to halt the chain reaction, remove singlet oxygen before releasing it as heat energy, engage in interactions with triplets or activated chlorophyll molecules in order to prevent singlet oxygen formation, and release additional energy via the lutein cycle. Particularly -tocopherol, tocopherol is a strong ROS scavenger in plants. To control the stabilisation of membrane lipids, it snares ROS and free radicals generated by lipid peroxidation. It has been discovered that flavonoids, which are active oxygen scavengers, can only function at or close to the location where ROS are formed, such as a vacuole or a cell wall. It has also been discovered

that osmotic regulating chemicals like proline and mannitol can scavenge ROS. To reduce the harm caused by salinity, plants scavenge ROS using both an enzymatic and non-enzymatic pathway.

Additional Physiological Control in Salt Stress

Ion compartmentation is a characteristic shared by all plants, as evidenced by the fact that it occurs in both non-halophytes and halophytes. In comparison to non-halophytes, halophytes have a distinct ion separation function. Halophytes frequently segregate the absorbed saline ions from the cytoplasm and store them in vacuoles to protect the cellular material from the toxicity of salinity ions. Non-halophytes, on the other hand, often decrease the absorption of harmful saline ions, protecting young tissues at the expense of old tissues, while transferring consumed salt ions to old tissues for storage. The compartmentation of saline ions depends on the trans-membrane proteins PPase, Ca^{2+}-ATPase, H^+-ATPase, secondary transporters, and several ion channel proteins. The H^+-ATPase and H^+-PPase on the membrane or vacuolar membrane produce the transmembrane potential gradient by first generating energy by breaking down ATP or pyrophosphate (PPI) to pump H^+ out of the cell. Na^+ is then transferred into the cell along the potential gradient via the proton's pumps-related Na^+/H^+ antiporters on the cell's membrane and vacuolar membrane. Ions may also be transported into the vacuole in order to decrease the osmotic potential in the cytoplasm. Salt stress reduces the function of the Na^+/H^+ antiporter, although this impact can be mitigated by boosting the level of unsaturated fatty acid in the cell membrane. The osmotic potential of the vacuole and the damage that Na^+ causes to the cytoplasm are both considerably decreased by the Na^+/H^+ antiporters that ensure Na^+ separate compartments in the vacuole.[35]

The three pathways that higher plants employ to assimilate carbon are the C3 pathway, C4 pathway, and crassulacean acid metabolism (CAM) pathway. In comparison to C3 plants, C4 and CAM plants are more resilient to stress in challenging situations like salt and drought while maintaining higher rates of photosynthesis and water usage efficiency. C4 or CAM metabolic can be induced by C3 metabolism in the interim. When phosphoenolpyruvate carboxylase (PEPCase) is triggered by a significant amount of Cl, the C3 pathway can change into the CAM pathway.

Mesembryanthemum crystallinum, a C3-CAM plant, switched from the C3 mode to the CAM mode in high-salinity soil to minimise water loss throughout the day.[36, 37]

One of the traits of higher plants' salt tolerance is the presence of salt vesicles. It is a type of trichome-derived big, extremely vacuolized cell. Salt vesicles vary in size and shape depending on the species. The stalk cells (SC), epidermal cells (EC), and epidermal bladder cells (EBC) that make up the EC-SC-EBC complex, which is what makes up the salt vesicle of Chenopodiaceae plants, are all three types of cells. The main functions of salt vesicles in plants include storing excess salt, water to protect plants from short-term osmotic stress, organic osmolytes, ROS scavengers, photosynthetic protein, and other things. Even though it has only been done at the cellular level, a sizable amount of the mechanism of the salt vesicle has been revealed. Because it isn't complete, the mechanism of the entire salt secretion process needs to be improved. There isn't much research on the formation of salt vesicles at the molecular level. It has not been possible to identify the essential genes that govern salt vesicle generation. It is also important to consider whether the genes connected to those governing salt vesicle development are linked to salt tolerance (Fig. 3).
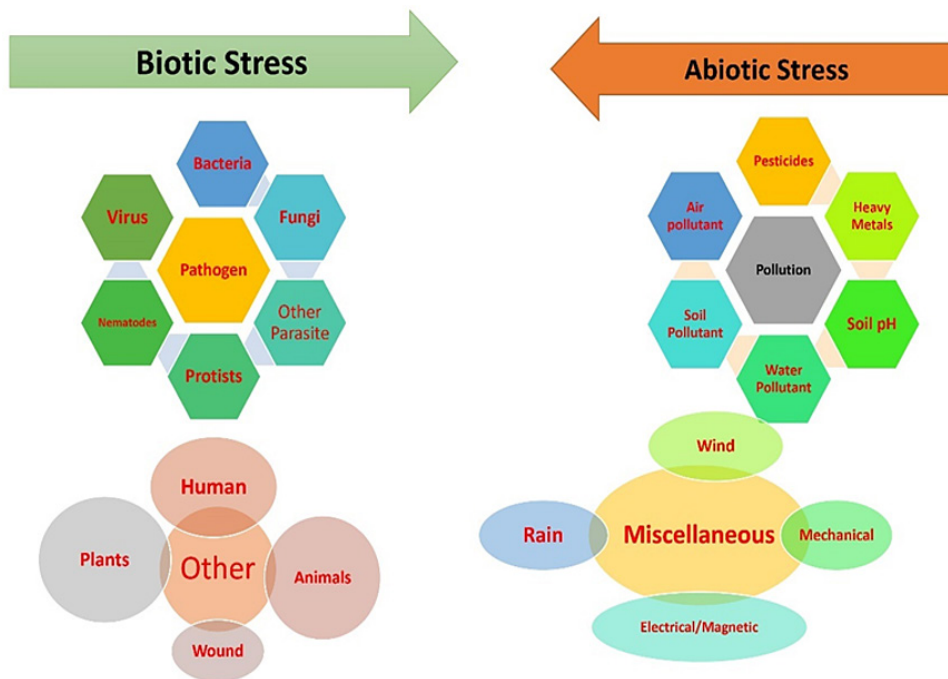

Fig. 3: Causes of Stress

Mechanism for Transducing Salt Stress Signals
A complex network of stress-inducible signals intersects during salt stress to control the physiological response of plants to salt stress. It has been investigated which signal transduction mechanisms in plants respond to salt stress. They can be categorized into two groups,

•   a Ca2+-dependent signal transduction pathway (SOS pathway, ABA pathway, and CDPK pathway), and

•   a Ca2+-independent signal transduction pathway, depending on whether Ca2+ is involved in the process (MAPK pathway).

Ca2+-Dependent Signal Transduction Pathway
Plant cells experience a rapid rise in Ca2+ content while under salt stress. Long recognised as both an osmotic regulator and a signal molecule involved in salt-induced signal transduction, Ca2+. The change in Ca2+ concentration in cells is the major

factor influencing Ca2involvement +'s as a second messenger. On cell and organelle membranes, a number of Ca2+ pumps, Ca2+ channels, and H+/Ca2+ antiporters control the inflow and outflow of Ca2+ in plant cells. As a result, cells have the flexibility to control variations in Ca2+ intensity and concentration as well as to initiate a variety of signalling cascades.

SOS Pathway

When plants are exposed to excessive salinity, high-affinity potassium transporters (HKT) and non-selective cation channels (NSCC) allow a significant amount of Na+ to enter the cytoplasm. Ion poisoning can occur in cells when there is a high level of Na+ in the cytoplasm. SOS signal transduction is the primary method by which plant cells release Na+ from the cytoplasm or separate Na+ into vacuoles. The Na+/H+ antiporter is situated on the plasma membrane and is encoded by the SOS1 gene in *Arabidopsis thaliana*. It participates in both Na+ transport from the root to shoot and Na+ excretion at the cellular level. A Ser/Thr protein kinase having a catalytic region at the N-terminal and a regulatory region at the C-terminal is encoded by the SOS2 gene. The SOS3 gene produces a protein that binds Ca2+. To stimulate the activity of SOS2 kinase, the SOS3 protein can bind with the regulatory region at the C-terminal of the SOS2 protein. SOS1 is phosphorylated by the activated SOS2 protein, which consequently increases SOS1's transporter activity.

Due to the SOS signal transduction system, a high external Na+ level causes a rise in internal Ca2+. SOS3 first binds to Ca2+ before attaching to SOS2. To make SOS2 kinase active, SOS3 turns off SOS2's self-inhibition. The SOS1 transporter, which is situated on the plasma membrane, is subsequently phosphorylated by the complex of SOS3 and SOS2, improving its capacity to transport Na+ out of the cell.[38] Another Na+/H+ antiporter found on the vacuole membrane is NHX1. By using a proton gradient, it can transport K+ as well as Na+ into the vacuole. In addition to participating in the salt response mechanism, the protein NHX1 also regulates the pH in the vacuole, vesicle trafficking, K+ concentration, and protein localization. Na+ entering vacuoles is regulated by NHX1, which is also regulated by ABA, through SOS kinases. The vacuole membrane contains several H+-ATPases

and H+-PPases to promote Na+ categorization because NHX needs a proton gradient to provide energy during Na + transport. The SOS3 is not essential for the process that transfers Na+ into vacuoles. The SOS3 homologous protein ScaBPs can also function similarly.[39]

ABA Pathway

In response to stress, plants store ABA, which is an essential part of many signal transduction pathways that participate in the stress response. Salt stress initially promotes ABA synthesis by regulating the translation of the ABA synthase genes through a Ca2+-dependent signalling mechanism. Through a process of positive feedback, the ABA generated by this method can promote ABA synthesis even more. The primary source of ABA build-up in roots is salt stress. In addition to helping the rhizosphere respond to salt stress, ABA can go via the xylem to active growth zones. After then, ABA will be reallocated within plants depending on the pH values of different environments. Following redistribution, the main ways that ABA reacts to salt stress are by regulating the opening of stomatal pores and triggering genes that provide resistance.

ABA can directly regulate the expression of the linked genes without the need for Ca2+. In the absence of ABA (SnRK2s), the phosphatase ABI1-insensitive1 (ABI1) inhibits the function of SNF1-related protein kinases (subfamily 2).[38] ABI1 is suppressed when a PYR/PYL/RCAR family protein interacts to ABA generated as a result of abiotic stress, which is how the PYR/PYL/RCAR family proteins sense ABA. When SnRK2s are unrestrained, numerous transcription factors belonging to the ABA-responsive element-binding protein (ABF) family are activated. ABFs then regulate the expression of several stress-related genes. It can also be made into a Ca2+ signal to achieve indirect regulation. By promoting the opening of certain Ca2+ channels on the membranes of the plasma and vacuoles. The cytoplasmic level of calcium is increased by ABA.[26] Then, Ca2+-dependent phosphorylation, which are in turn suppressed by 2C-type protein phosphatases (PP2C), cause OST1 (ABA-activated SnRK2 protein kinase open stomata 1) to be activated. OST1 additionally regulates the activity of the guard cells' K+ channel KAT1 and SLAC1 anion channel (slowly activating anion conductance 1) in order to seal the stoma.

CDPK Pathway

Ca2+-dependent protein kinases (CDPKs) are abundant in plants. Depending on the subcellular location, CDPKs can exist in membrane-bound or membrane-free cells. The bulk of them are present in the plasma membrane and organelle. They are involved in both the regulation of the development and growth of plants as well as the process of resistance to abiotic stress. It is widely acknowledged that CDPKs largely govern plant tolerance to salt stress by controlling stomatal opening and the expression of ion channel-related genes. In a number of plants, the transcription factors involved in signal transduction that the CDPK genes encode boost the activity of the protein enzyme and other subsequent signalling elements. CDPKs can also modify the equilibrium of ROS, affecting how plants respond to oxidative stress and enhancing their tolerance to salt by encouraging the expression of antioxidant genes and inhibiting NADPH oxidase [36].

Ca2+-Independent Signal Transduction Pathway (MAPKs Cascade)

One of the most important signal transduction pathways in plants is protein phosphorylation, which is mediated by protein kinases and enables MAPK cascades to gradually boost environmental signals. It can send a message from a receptor on the cell's surface to the DNA in the nucleus. The components of MAPK cascades, which are in turn initiated by phosphorylation, are three protein kinases designated MAPKKK (MAP kinase, kinase, kinase), MAPKK (MAP kinase, kinase), and MAPK. MAPKKK is the most upstream protein kinase in the MAPK cascade, which is started by signals supplied by receptor kinase on the membrane of the cell by phosphorylation.[37] By phosphorylating the S/T-X3-5-S/T motif in the conserved region of MAPKK, MAPKKK activates MAPKK (S represents serine, T represents threonine, X represents any amino acid, and 3–5 represents the number of amino acids). By phosphorylating the serine/threonine and tyrosine residues located between MAPK's seventh and eighth subdomains, MAPKK causes MAPK to become active [35]. The most downstream component of the entire cascade, MAPK, reaches the nucleus and stimulates the activity of particular transcription factors to cause the production of relevant functional genes, causing plant cells to undergo a variety of physiological and biochemical processes. The MAPK cascade is capable of transducing a wide variety of signals, including ROS signals. Plant cells recognise ROS signals through certain receptors when they are under osmotic stress. Once ROS has been detected, it triggers Ca2+ signalling, activates protein kinase Oxl1 (Oxidative signal-induced kinase 1), and then initiates the MAPK cascade. To govern the physiological response of plants to salt stress, there is an intricate network made up of multiple stress-inducible signal pathways. The SOS route, CDPK pathway, MAPK pathway and ABA pathway are the only four pathways that are more well-known to us and that play more important functions.[42, 43] In recent years, more and more components associated with salt stress signal transduction have been identified, yet there are still a number of unanswered questions. The selectivity and interconnections of the several signal transduction pathways in salt-stressed plants are still very poorly understood.

Antioxidant-Related Genes

Salt stress results in the production of a large amount of ROS. By increasing gene transcripts for antioxidant proteins including CAT, APX, ROS and SOD, POD, can be quickly eliminated.[44] In recent years, various plant anti-oxidant enzyme gene families' variable expression under environmental stress has been investigated. Brassica juncea and B. rapa's abiotic-stress response SOD gene family was identified and characterised genome-wide.[45, 46] The class III POD gene family in cassava was identified and its expression was examined.[47] The Cotton CAT gene family genome-wide and conducted a bioinformatics analysis.[48] A genome-wide study and profiling of expression of the APX gene family in Gossypium hirsutum.[49]

In addition to the families of genes that code for antioxidant enzymes, there are other genes related to antioxidants. AsA and GSH are two more important antioxidants found in plants. They can perform synergism and regeneration during the AsA-GSH cycle. Important proteins in this cycle can be overexpressed to enhance AsA and GSH production, which would increase the ability of plants to survive oxidative stress. GSH is produced by two processes in plants. After glutamate cysteine ligase (GCL) first catalyses Glu and Cys to form -glutamyl cysteine, Glutathione Synthase (GS) catalyses Glycine and -glutamyl cysteine to produce GSH.

APX oxidises AsA to produce MDHA in addition to aiding in the detoxification of H2O2. Additionally, MDHA can transform into DHA on its own or into AsA with the help of MDHAR. DHAR then transforms DHA into AsA. Other important enzymes include GR, GSTs, etc. For instance, researchers revealed that AtGSTF8 and AtGSTU19 functioned in the root to fine-tune the redox homeostasis, contributing to *Arabidopsis* salt stress tolerance. CAR's primary function is to eliminate ROS generated during photosynthesis. CARs come in a variety of forms. As a result, each step of their various manufacturing processes uses a distinct enzyme. Transgenic *Arabidopsis* shown a greater tolerance to drought and salt stress when the Cerasus humilis ChVDE gene, which expresses a violaxanthin de-epoxidase, was overexpressed.[50, 51, 52]

Signal Transduction-Related Genes
According to earlier studies, the *Arabidopsis* SOS gene family has six genes that are either directly or indirectly related to salt tolerance. SOS3 and SOS2 located in the cell's cytoplasm can govern SOS1 on the plasma cell membrane, enhancing salt tolerance by regulating the ion equilibrium of K+ and Na+. SOS1, a member of the SOS family, is a gene specifically linked to plant salt tolerance. By controlling the activity of SOS1 and other ion transporters as well as the growth of root hair during salt stress, SOS4 improves salt tolerance. The SOS5 protein, which is situated outside of the plasma membrane, is essential for the creation of cell walls and cell junctions. SOS6 is crucial in controlling oxidative and osmotic stress in cells. At the same time, significant progress has been made in locating SOS gene families in many plant species.[53] The genome-wide identification, gene expression and the analysis of the SOS family genes described in Brassica juncea var. tumida. and SOS family genes in Spinacia oleracea.[54, 55]

By responding to Ca2+ and triggering reversible protein phosphorylation, ABA modulates plant salt tolerance in the ABA signalling pathway. Salt stress response genes' expression can be controlled by Ca2+-triggered protein kinases. A class of proteins called regulatory proteins known as ABFs/AREBs (ABRE binding factors) govern the functioning of identical genes by binding with ABA-responsive elements (ABRE), which in turn controls ABA-dependent gene expression. Since

ABA indirectly stimulates these AREBs, it is believed that overexpressing them can boost plants' tolerance to abiotic stress,[28] the PpSARK (Senescence-associated receptor-like kinase) favourably regulates the salt stress response in Physcomitrella patens via an ABA-related pathway.[28, 57-62] The OsNAC45 is essential for rice's ability to respond to ABA signals and tolerate salt. OsMADS25 may be a crucial transcription factor that controls rice root growth and salt tolerance via ABA-mediated regulatory pathways and ROS scavenging.[63,64] Protein kinases are essential signal transducers that control how plants respond to abiotic stress, in particular CDPKs and MAPKs. The CDPK gene families of several plant species have been identified and characterised. In *Arabidopsis thaliana*, 34 CDPK members have been identified, the majority of which function in stress signalling. Ion flow investigations revealed that cpk27-1 mutants with increased susceptibility to salt stress had worse capacities for Na+ excretion and H+ uptake than wild-type plants following extended salt treatment, indicating that AtCDPK27 is implicated in *Arabidopsis*' reaction to salt stress. Na+ levels in the roots of cpk12-RNAi plants increased and were higher than those of wild-type plants after NaCl treatment, indicating that AtCPK12 was necessary for plants to respond to salt stress. Under salt and drought stress, AtCPK6 is implicated in the positive regulation of methyl jasmonic acid signalling in guard cells. By phosphorylating the 261st serine residue of CAT3, AtCPK8 interacts with CAT3 and controls the activity of CAT3, which controls how well plants can scavenge ROS. Some plants have been found to include MAPK members linked to the response to salt stress over the past 20 years. In *Arabidopsis*, AtMEKK1 phosphorylates AtMKK2 and AtMEK1 in response to severe salt stress, activating downstream kinases AtMPK4 and AtMPK6. In Populus trichocarpa PtMAPKK4 overexpression enhances tobacco's tolerance to salt.[65, 66] The stress-tolerant seedling growth was better when the Vitis viniferaVvMKK2 and VvMKK4 genes had been elevated in transgenic *Arabidopsis thaliana*. Whereas overexpressing VvMKK4 only boosted the tolerance to salt stress, overexpressing VvMKK2 increased *Arabidopsis*' tolerance to both drought and salt stress. Genes of Zea mays ZmMKK4, Gossypium hirsutumGhMAP3K40, Gossypium hirsutumGhMPK2, and other genera that are overexpressed can improve how resistant transgenic

plants are too high salt and alkali concentrations.[67, 68, 69]

Regulatory Genes

Salt tolerance is a quantitative genetic feature that is controlled by a number of genes. Transcriptional factors control how much each gene expresses by changing how it does in response to salt stress. Numerous families of core transcription factors, including WRKY, bZIP, MYB, AP2/ERF, CBF, DREB, NAC and bHLH have been reported. The stress-responsive genes GmGST1, GmLEA, GmWD40, GmDHN15, and GmMYB48, may express more when GmbZIP2 is overexpressed in soybean hairy roots [70]. The enhanced salt tolerance of *Arabidopsis thaliana* is a result of the transcription factors bHLH and WRKY regulating the expression of AtKUP2. Through controlling ABA signalling pathways, Plant tolerance to salt stress is influenced by AtMYB20 in *Arabidopsis thaliana*. The AtMYB20 gene expresses in response to ABA and salt stress. Overexpression of the AtMYB20 gene lowers the expression of the AtPP2CA (a negative regulator of ABA signal), ABI1, and ABI2, genes during salt stress and boosts the salt stress resistance of transgenic *Arabidopsis*. Tamarix hispida's tolerance to salt can be improved by ThDREB transcription factor by boosting the activity of the plant's antioxidant enzymes.[16] In addition to other salinity-stressed parameter alterations, overexpressing SlMYB102 in the Solanum lycopersicum L. enhanced K+/Na+ ratios and raised ROS scavenging enzyme activity. Several salt stress-related genes, including SlNHX3, SlNHX4, SlHAK5, SlSOS1, SlSOS2, SlCPK1, and SlCPK3, had their transcript abundance increased in two OE lines under salt stress, according to the results of the qRT PCR analysis.[71] The over-expression of VvNAC17 increases *Arabidopsis thaliana* plant resilience to salinity and drought while up-regulating the expression of ABA and stress-related genes such as COR47, ABI5, COR15A, AREB, and P5CS.

In addition to the transcription factors, several regulatory genes are linked to plant salt tolerance. Many short non-coding RNAs, such as microRNAs (miRNAs), have emerged in recent years as crucial regulators of chromatin remodelling, translation inhibition, and mRNA degradation. The metabolic route, the ubiquitination pathway, transcription factors, signal transduction elements, and genes involved in RNA processing and protein synthesis are among the target genes of miRNA. Transgenic Osa-miR393a increased K+ uptake while improving salt stress tolerance as compared to wild-type controls. The *Triticum aestivum* plant response to salt stress and Pi starvation is mediated by TaemiR408, which targets six genes that encode proteins involved in biochemical metabolism, microtubule assembly, and signalling transmission.[72]

Although research on the genes responsible for salt tolerance in plants has advanced quickly recently, it is still mostly focused on locating and modifying the homologous genes responsible for salt tolerance in *Arabidopsis*. It is possible to find new salt-responsive genes using an appealing method. Halophytes can be studied using comparative genomics or transcriptomics to discover new genes that react to salt. Some potential genes for salt tolerance in the halophyte Atriplex canescens used transcriptome.[43, 73] It is anticipated that as sequencing technology develops quickly, more and more sequences of genomes will be made available, which will prove useful for molecular breeding in the future even though full genome information is necessary for comparative genomics and transcriptomic investigations.

Methods for Improving the Tolerance of Plants to Salt

There have been numerous methods described so far to increase a plant's tolerance to salt, and these can be divided into two sets: genetic improvement. and non-genetic improvement.

Genetic Improvement Techniques

Genetic engineering, which adds salt stress-related genes into the plant, is the simplest and most effective method of boosting a plant's salt resistance. The tobacco osmotin gene, in addition to those genes listed in the section before, has recently drawn a lot of interest because of its potential to benefit plants that are suffering from salt stress. Plants respond to a variety of biotic and abiotic stresses by producing a protein called osmotin, which has multiple functions. It belongs to the family of pathogenesis-related (PR) proteins known as PR-5. It protects plants by reducing the production of ROS, reducing lipid peroxidation, initiating programmed cell death (PCD), and increasing proline content and antioxidant enzyme activity. According to

studies, transgenic plants that overexpress the tobacco osmotin protein are protected from various stresses, such as salt stress and fungus infections. The putative transgenic Capsicum plants used to demonstrate higher salt tolerance but were morphologically similar to wild-type plants.[74,75] The same results were obtained when the tobacco osmotin gene became overexpressed in soybean plants. The improved salt tolerance produced by tobacco osmotin protein overexpression in Olive may be related to the transgenic plants' sulphur metabolism.[76, 77] Even though there is some evidence that the Nicotiana osmotin protein promotes plant stress tolerance, the full mechanism of osmotin activity is still not fully understood and has to be elucidated. Plant salt tolerance is regulated by a complex network of levels and genes. Plants' capacity to tolerate salt can be improved by utilising a single transgenic approach, such as increasing the concentration of a specific osmolyte or the activity of a certain oxidase. However, development is limited in scope. As a result, we must determine how to prioritise each tactic. When trying to increase a plant's resistance to salt, it is best to prioritise our strategies to obtain better results.[78]
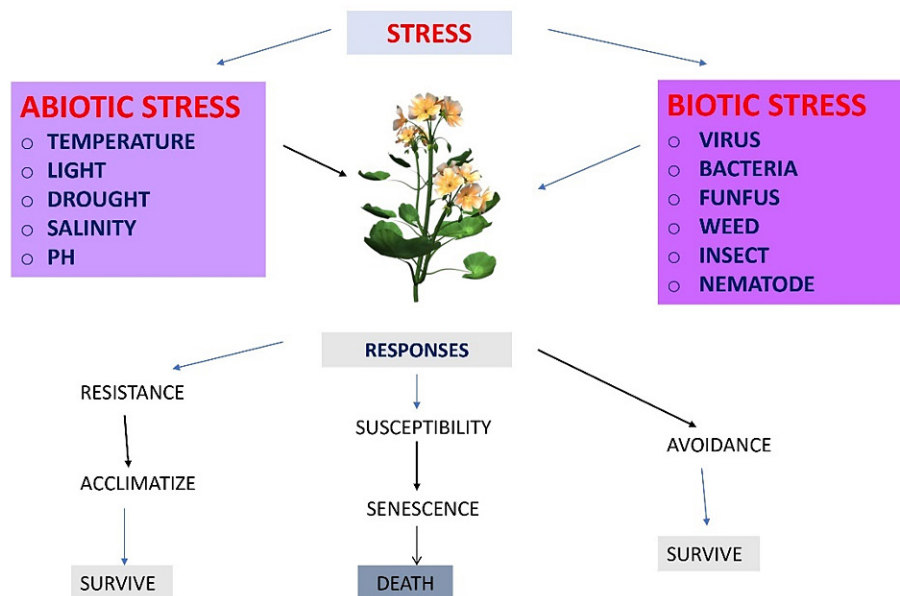

Fig. 4: Overview of Stress

Non-Genetic Improvement Techniques

A successful method for raising a plant's tolerance to salt is through conventional breeding. New salt-tolerant plant types can be developed by recurrent cutting, grafting, artificial selection, hybridization, tissue culture, and other asexual propagation methods. Exogenous chemical application can also improve a plant's resistance to salt stress. Common exogenous substances fall into several categories: those that act as osmotic regulators, such as gibberellin, sugar betaine, and organic acids; those that promote plant growth; those that can stimulate the activity of antioxidant enzymes in plants, such as selenium, silicon, NO, etc.; and those that decrease cell membrane permeability, such as humic acid, Ca2+ and salicylic acid. for instance, under salt stress, plants treated with exogenous melatonin displayed stronger antioxidant enzyme activity, lower rates of electrolyte leakage, higher photosynthetic rates and lower MDA contents than the control group, suggesting that melatonin may improve plant salt resistance by increasing photosynthetic capacity, oxidation resistance, and ion homeostasis.[79] Another new strategy has attempted to use the interaction of fungi and roots to create symbionts with particular structures and functions to increase the salt tolerance of plants. The impact of systemic fungal endophytes, which were isolated from plants growing naturally in salinized soil, on plant resistance to salt. The findings demonstrated that compared to non-colonized plants, endophyte-colonized plants exposed to salt had higher root and shoot biomass,

better water usage efficiency, higher photosynthetic efficiency, and lower ROS levels. The harm caused to plants by salt stress can also be efficiently reduced with rational fertilisation. Phaseolus vulgaris, for instance, was able to tolerate salt better thanks to fertiliser phosphorus.[80, 81]

Conclusions and Perspectives

In conclusion, research into how plants react to stress is expanding quickly, but there are still a lot of unanswered concerns. It is crucial for agriculture, the environment, and the survival of all living beings to comprehend how plants react to stimuli. With a focus on the low-level effects that deviate from conventional linear models and lack a distinct threshold in the dose-response relationship, I have gathered information on both the effects found at low doses or concentrations (referred to as non-target effects) and the direct effects of high doses or concentrations of stressors on plants (referred to as target effects). Plants can adapt and become more resilient as a result of prolonged exposure to stresses, which increases their resistance. The details offered can help plant scientists recognize and investigate these phenomena to more fully comprehend the mechanisms underlying plant stress responses. By comprehending this reaction, which is a built-in characteristic of the natural world, we may anticipate the repercussions of excessive chemical use in agriculture and the prospective effects of untested compounds.

Over the past 20 years, a lot of effort has been made to understand the inner workings of plant salt tolerance. There is, however, still a tremendous amount of room for further investigation and learning. To begin with, it is yet unknown how salt stress impacts plants' ability to synthesize food. There hasn't been any progress toward agreement so far. It is necessary to conduct more research on the combination of morphological, physiological, and molecular techniques for plant stress detection. The peculiar salt-tolerance mechanisms employed by halophytes, such as salt vesicles, remain largely unexplored. Little is known about how salt stress affects plants and how different signal transduction pathways work together when they are under salt stress. Comparative genomic and transcriptome methods may become more important in the future to pinpoint the genes that respond to salt stress. In order to get superior improvements, we must ultimately decide how to prioritize each improvement technique (Fig. 4).

Conflict Of Interest

None

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