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Review

Recent Advancement on Physiological and Molecular Response to Cotton under Salt Stress: A Review

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Abstract: Soil salinity is a serious issue that is spreading worldwide because it inhibits plant growth and development and reduces crop yield. Because soil salinization has evolved as a global issue, understanding the mechanisms underlying cotton plant ability to tolerate is essential for increasing cotton crop yield, breeding new salt-tolerant varieties, and making the most of saline land. Based on previous research, our review discussed the effects of salt stress on cotton, such as photosynthetic activity reduction, ion homeostasis disruption, membrane peroxidation occurring and healthy growth. Reactive oxygen species scavenging and osmotic, two critical physiological mechanisms for salt tolerance, have also been summarized. Primary signalling pathways associated with salt stress hypersensitive protein kinase, calcium-dependent protein kinase, and mitogen-activated protein kinase. We have described the current strategies and methods for enhancing plant salt tolerance. In conclusion, we covered the aforementioned topics hoping they would be useful backgrounders for future agricultural work in the cotton region.

Keywords: cotton; salt stress; functional genomic; antioxidants; salt-related Genes functions

1. Introduction

Cotton (Gossypium hirsutum L.), is a cash crop for the textile industry, and contributes to 35% of the total fiber consumed globally (Salimath et al., 2021). China is considered as a leading country regarding cotton production followed by India, USA, Brazil and Pakistan (Ahmad et al., 2022). During growth and development, cotton crops are frequently subjected to abiotic stresses, which limits the lint yield and fiber quality (Zhang et al., 2021). Salt stress is the main hindrance to cotton production globally. Identification and functional characterization of salt-tolerant genes, molecular breeding, and understanding the functions of exogenous hormones under salt stress have become hot topics for researchers.

Salt stress affects over 30% of the world's arable land, and this problem worsens continously (Pitman and Läuchli, 2002;Shrivastava and Kumar, 2015). According to adaptive evolution, there are two major categories of plants: glycophytes and halophytes (which can tolerate salinity) (Abobatta, 2020). Salinity stress could severely influence on metabolic and physiological mechanisms and eventually reduce crop yields (Salwan and Vivek, 2023). The well-known process by which soil salinity affects plant development is initially through osmotic process and ion toxicity (Babayev et al.;Nadeem et al., 2022). One of the most alarming environmental problems of the twenty-first century is soil salinity (Phour and Sindhu, 2023). It is an important to explore the prospective solution to combat the soil salinity threats (Fróna et al., 2019). Currently ,only two main strategies for reducing soil salinization are utilizing chemical additives to repair soil degradation and applying recent advanced biotechnology tools to develop salt-tolerant plant varieties (Ashraf and Wu, 1994). When

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comparing these two techniques , the former method considered as a expensive and causing secondary salinization risk (Stigter et al., 2006). The ability of cotton plants to tolerate salinity varies genetically depending on the species. Cotton plant biologists can describe physiological mechanisms, pairs of genes, and transcription factors concerned with stress tolerance and combine them into selected crops to generate salt-tolerant cotton plants with various levels and variable responses to salinity stress.

A specific, as of yet unidentified Na^+-sensing module recognizes Na^+. Early perception is followed by the induction of upstream signalling g expressions. The complicated signal transduction network includes the following molecules: K^+, Ca^{2+}, H^+, phospholipid, ROS, different protein kinases, and plant hormones. Transcriptional elements that control stress-responsive genes are subsequently activated. Functional genes, such as those for ion transporters and antioxidants, are consequently effectively expressed. Inference-based reactions, such as ROS scavenging, are explained by plants that can withstand and adapt to salt stress. In plants to develop resistance, each link in the chain is crucial. To address this, we can modify plants grown in saline soil. To use comparable techniques on plants that are not salt-tolerant, Scientists are investigating salinity tolerance mechanisms in salt-stress plants (Liang et al., 2018) (Figure 1).

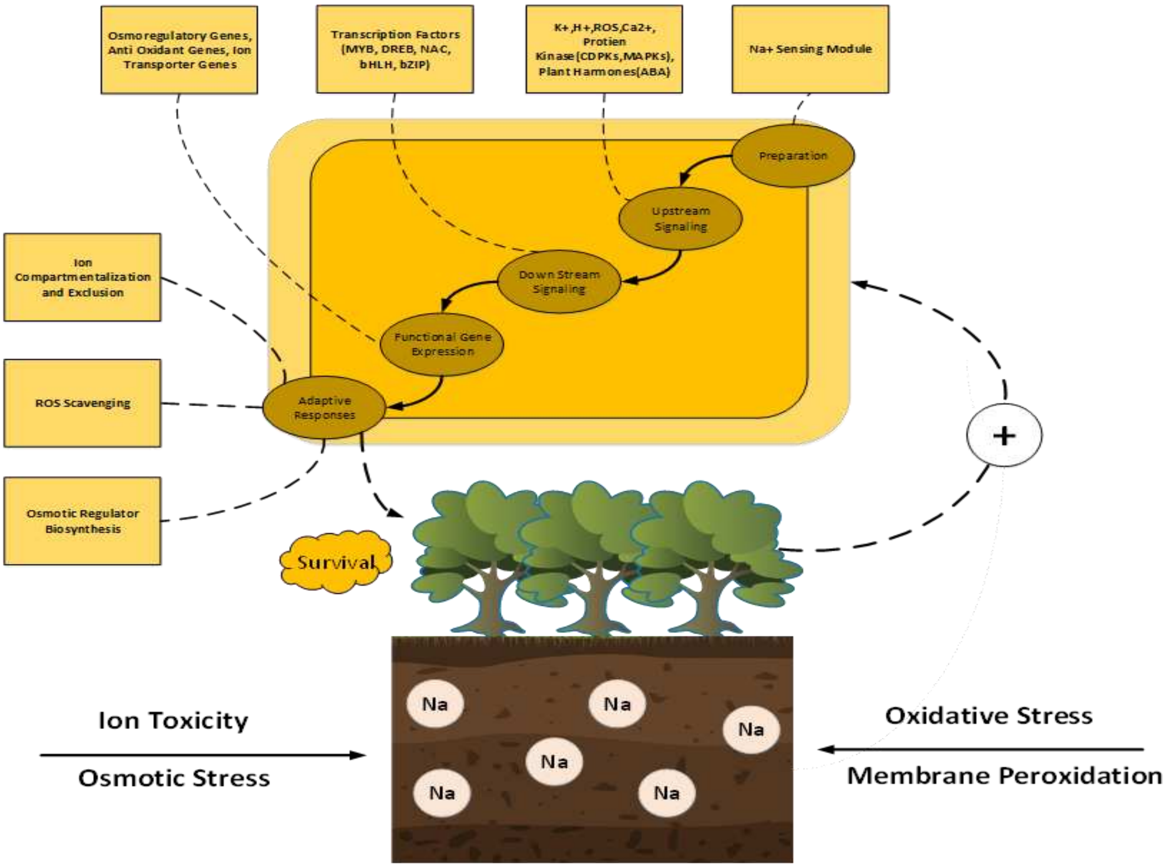

Figure 1. The general diagram describes the developing process of salt tolerance in plants.

The objective of current review is to present a brief overview on the situation of the art research on plants under salt stress. We described how cotton plants could become damaged by salt, the mechanism of salt stress signalling, and the mechanism used by cotton plants to withstand salinity in this review paper. The current study will help the readers better understand the background knowledge on cotton plants under salt stress. In addition, we offered our opinions on the future course of this field's study.

2. Salonization in cotton

Salinity stress alters the physiological activity of the seed, which has a detrimental influence on seed germination (Ibrahim, 2016). Salinity reduces food storage , protein content, and water potential in various plant seeds During germination (Wu et al., 2019). Salt stress decreased phosphatase activity in *Arabidopsis thaliana* seeds, ultimately leading to inhibiting seed germination (Shi et al., 2003). By lowering the amount of gibberellic acid (GA3), and raising the composition of soluble sugar, and starch in cotton plants, the germination rate was reduced by salts (Bai et al., 2020). Cotton plant development and the formation of its essential components are significantly impacted by salinity stress (Brugnoli and Björkman, 1992). Biological mass, foliage area, yield, stem length, and root length all declined in high-saline soil (Arif et al., 2020). The growth parameters, including, the percentage of lint yield, the weight of the cotton ball, the number of cotton balls made per plant, and the crop quality are all significantly impacted by soil salinity (Sabagh et al., 2021).

The previous study indicated that cotton plants exhibit delayed growth, reduced branch growth, decreased plant height, lower germination rate, and wilted leaves when exposed to salt stress (Qin et al., 2022). Due to the salinity, the mechanisms of osmotic pressure become disturbed, which inhibits plant growth (Safdar et al., 2019). Ion toxicity is what happens when too many salty ions enter a plant's transpiration stream and interruption of photosynthesis, deterioration of ion homeostasis, and oxidation of membrane lipids all harm plant cells (Hasanuzzaman et al., 2013). In conclusion, understanding how plants physiologically to salt stress are essential for increasing plants' tolerance to salts (Figure 2).

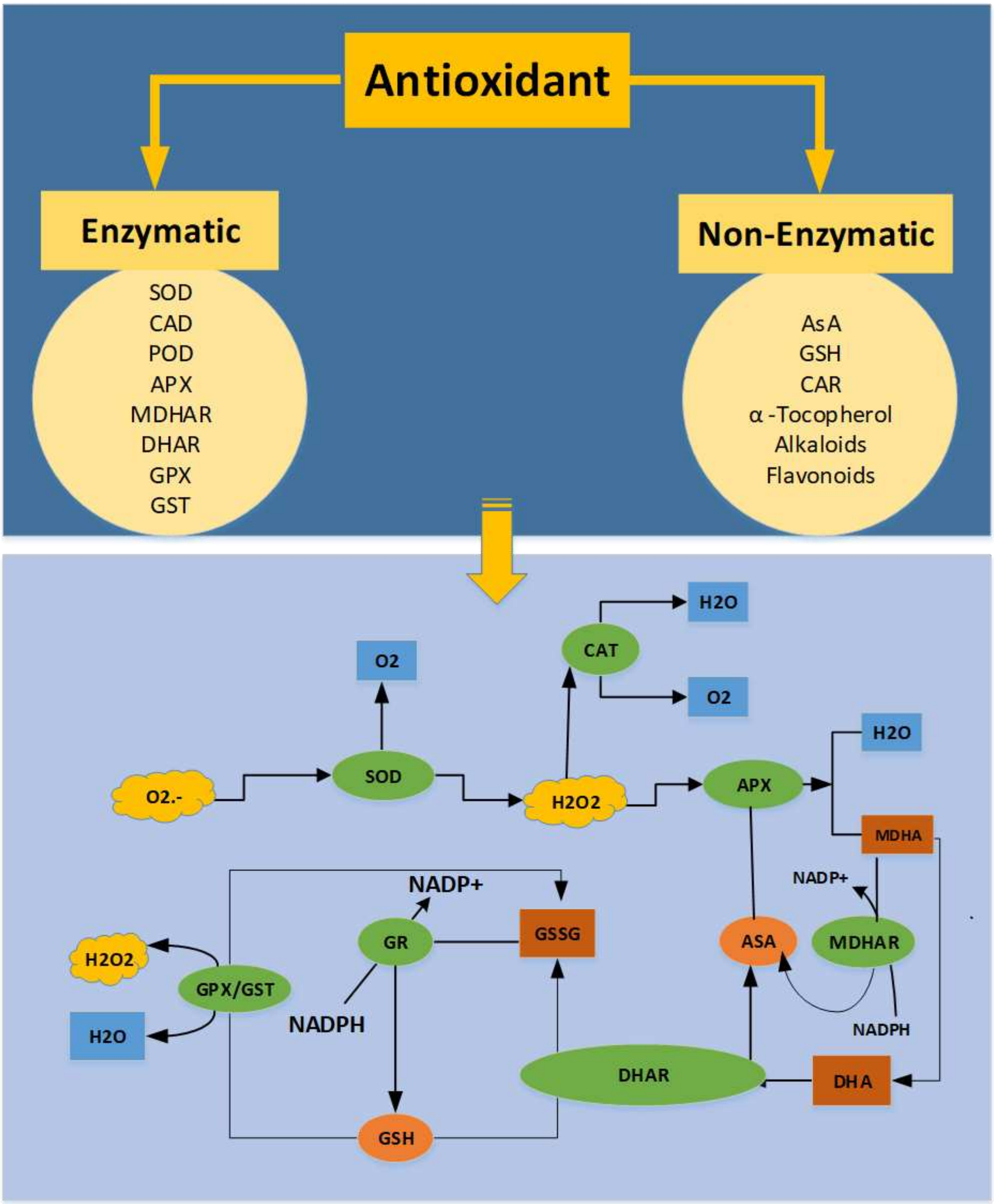

Figure 2. The mechanism of salt-related plant injuries.

3. Salonization and Photosynthetic activity in cotton

3.1. Effect of salinity on stomatal conductance

Salinity hinders gas exchange and lowers stomatal conductance, which decrese the rate of photosynthetic activity. Due to the salinity halophyte grasses produce less photosynthetic pigments. High accumulation of salinity in broccoli results in decreased indicators of photosynthetic activity, total chlorophyll contents, and grana-reducible chloroplast structural degradation (Del Amor and Cuadra-Crespo, 2011;Hamza and AL-Taey, 2020). Increasing salt concentrations significantly impact Chickpea's photosynthetic electron transport chain (Çiçek et al., 2018). Due to high salinity levels, transpiration, photosynthesis, chlorophyll contents, and stomatal conductance were decreased in different pomegranate genotypes (Soori et al., 2019). Moreover, lowering carboxylation results in a decrease in mesophyll conductivity. Reduction of photosynthetic apparatus lead to reduced photosynthetic capability and photosynthetic characteristics because of soil salinization (Mbarki et al., 2018). High salt contents caused abnormalities in stomata structure, leading to shortened chlorophyll pigments, further reducing photosynthesis (Yildiztugay et al., 2020). salinity significantly influenced net photosynthesis, the Fv/Fm ratio, stomatal conductance, and rocket plants' transpiration rate (Hniličková et al., 2017).

3.2. Salinity influence on total chlorophyll contents

High salinity decreases the amount of total chlorophyll, chlorophyll fluorescence, and Rubisco activity in maize. Additionally, it alters the shape of the chloroplast and stomata (Xu et al., 2018). In mustard, prolonged soil salinity decreased photosynthetic properties, particularly by reducing PSII (Fv/Fm) activity (Wani et al., 2019). In lisianthus cultivars, salinity decreased gaseous exchange and transpiration (Ashrafi and Rezaei Nejad, 2018). Total closure and a decrease in photochemical and carbon metabolism are two ways that salinity inhibits photosynthesis (Ju et al., 2023). High salinity drastically reduces PSII photochemistry's maximum quantum yield (Liu et al., 2023b). As a result, salinity in cotton plants decreases photosynthesis, chlorophyll fluorescence, transpiration, and stomatal conductance by degrading ultrastructure, chlorophyll, and carotenoid **production.**

3.3. Osmotic pressure affected by salinity

Salt stress has a major effect on the rate of photosynthetic activity, osmotic potential, water potential, transpiration rate, leaf temperature, and the overall water content of cotton plant leaves (Liu et al., 2023a;Naikwade, 2023). There were two negative impacts of salt stress on photosynthesis (Singh et al., 2022b). First off, salt stress causes plants' stomas to close, lowering the level of CO_2 in their cells (Yildirim et al., 2022). Second, the system of photosynthetic membranes is harmed by salt stress, which also reduces the ability to absorb CO_2, restrictions not connected to the stoma, like harmed photosynthetic pigments (Zahra et al., 2022). Specialized epidermal cells called a stoma, commonly called guard cells, create pores on the surface of cotton plant leaves (Wall et al., 2022). When the osmotic pressure within the cells falls, guard cell water outflow will result in stoma closure and the contraction of guard cells (Liu et al.). This often results in salt stress leaves having higher Na^+ and Cl contents, lower K^+ contents, and eventually closing their stomas (Jadidi et al., 2022). The reduced stoma opening significantly decreases the intercellular CO_2 concentration and photosynthetic rate, as well as CO_2 diffusion from the environment to the chloroplast (Zou et al., 2022).

3.4. Salt stress harms the components of photosynthesis

In addition to stomatal restrictions, salt stress harms several other components of photosynthesis but does not directly affect the stoma (Singh et al., 2022a). Chlorophyll, the main pigment involved in photosynthesis in salt-sensitive plants, usually decreases under salt stress. The same results were found after salt stress in rice (Somaddar et al., 2022), soybean (Begum et al., 2022), and pepper (Atzori et al., 2022), the ultrastructure of chloroplasts is similarly impacted by salt stress. The light reaction occurs on the thylakoid membrane, the most significant part of the chloroplast.

3.5. Salt stress influence on photosynthetic enzyme activities

The impact of salt stress extend to components of photosynthesis, especially the structural proteins and enzymes engaged in the transmission of photosynthetic electrons, the fixation of CO_2, and the absorption of light energy (Zahra et al., 2022). (Wei et al., 2022), found indicate a connection between the photosynthetic process and glucose-6-phosphate dehydrogenase (G6PDH). Interfering with the oxygen-evolving complex's ability to function, salt stress reduces electron transfer efficiency by preventing electron transfer from plastoquinone A (QA) to plastoquinone B (QB), and by impairing the function of the pigment-protein complex on the thylakoid membrane (Sghaier et al., 2022;Yan et al., 2022). Salt stress also affects rubisco, a rate-limiting enzyme in photosynthesis(Li et al., 2022a). Salt stress reduces Rubisco's activity and restricts the restoration of the compound ribulose-1, 5-bisphosphate (RuBP), which has an impact on plants' ability to take up and utilize CO_2 (Bhattacharya, 2022;Yang et al., 2022). According to previous research, salt stress prohibits salt-intolerant plants from photosynthesis due to stomatal and non-stomatal restrictions (Iqbal and Ashraf, 2005).

Some contend that stomatal closure results from physiological salt stress (Azevedo Neto et al., 2004). Moreover, some research has shown that salt stress does not cause reduce in photosynthetic activity to occur at the exact time as a decrease in plant water potential. It's a common misconception that stomatal closure doesn't appear to be brought on by a drop in leaf water potential (Williams et al., 2012). According to others, the feedback cycle resulting from plant development in salty soils restricts photosynthesis by raising the sugar level in plant tissues (Bernstein and Hayward, 1958;Ruiz-Lozano et al., 2012;Wang et al., 2023). This viewpoint, cannot explain the extremely low glucose concentration found in perennial woody plant stems that have been exposed to persistent salt stress. Consequently, a greater investigation is required into how salt stress is decreased by photosynthesis in plants (Hashemi et al., 2023).

4. Ion Homeostasis Disruption

Mineral elements, which normally reside as ions in cotton plant cells, make up the structural elements of cells (Naz, 2023). Minerals serve as coenzyme and enzyme building blocks that regulate enzyme activity (Panda and Zhou, 2023). They also engage in the electrochemistry of charge neutralization, colloidal stabilization, and osmotic regulation (Hou et al., 2023). The harmonization of ion metabolism is required for the consistency of the cell membrane and the promotion of plant growth (Adhikari et al., 2023;Phour and Sindhu, 2023). The major sources of salt damage are an excess of Na^+ and Cl^+ and a corresponding lack of important ions like Ca^{2+} and K^+ (Isayenkov and Maathuis, 2019;Vivaldi et al., 2021) because there is so much Na^+ in the soil, it accumulates in plants. Lowered membrane potential and promoted Cl absorption along a chemical gradient are both effects of high Na^+ concentrations. High Na^+ concentrations prevent cell division and growth because they lead to osmotic imbalance, membrane dysfunction, and enhanced ROS production (Ahmad et al., 2019). Too much Na^+ can harm some enzymes and affect cellular metabolism (Nieves-Cordones et al., 2016). A high Cl concentration hinders plant growth, contributing to reducing the quantity of chlorophyll present and harming the organelle and cell membrane systems (El-Banna and Abdelaal, 2018). In addition to their toxic effects, Na^+ and K^+ compete since they have similar ionic radii and hydration energies (Kaya et al., 2007). To ensure their physiological function, the majority of cells maintain a cytoplasmic K^+ concentration that is quite high and a cytoplasmic Na^+ concentration that is relatively low (Leigh and Wyn Jones, 1984). As a result, a significant external Na^+ influx will stop K^+ from entering, preventing the K^+ deficiency that damages plants (Kumari et al., 2021). According to the researcher, that Na^+ competitive inhibition, the amount of Ca^{2+} in cells also drops (Rengel, 1992). Ca^{2+} is an important component in the signal transduction of some physiological mechanisms in crops. (Bernstein and Hayward, 1958), claimed that when there are high Na^+ concentrations present, plants can adjust their osmotic pressure compensating reduction in Ca^{2+}. Furthermore, (Dai et al., 2015) showed that salt stress decreases plants' capacity to absorb NH^{4+} and NO^3. In a nutshell, the ion balance in plant cells is upset by salt stress, which influences cotton plant progress and growth (Ashraf et al., 2018b).

5. Salt stress and Membrane permeability

The movement of chemicals, energy, and information transmission are all made possible by the cell membrane, which protects plant cells and serves as an essential protective barrier (Finkina et al., 2016). The cell membrane's capacity to control ion homeostasis in a specific way, and maintenance of plant physiological functions. However, increased ROS generation under salt stress causes significant membrane damage by raising relative permeability and lowering fluidity (Gill and Tuteja, 2010). However, it also produces many electrolyte exosmotic, leading to osmotic pressure problem.

Membrane-bound proteins and enzymes may become inactive due to MDA contents. MDA is a primary consequence of membrane lipid peroxidation, which could harm the biofilm's structure and functions (Pigeot-Rémy et al., 2012). The MDA contents in the plasma membrane is an important indicator of the extent of the damage. In previous study, it was observed that Carex rigescens' MDA content significantly increased following salt stress treatment (Li et al., 2018a).It was discovered that salt stress increased the MDA content of soybean. (Li et al., 2017) The establishment of the endoplasmic reticulum and the plasma membrane vacuole are just two examples of organelle structures within cells that increased ROS can harm. In other words, oxidation caused by excessive ROS formation due to salt stress, which prevents plant growth by damaging plant cells (Khan et al., 2011).

6. Characteristics of salt stress in cotton

The first physiological sign of salinity stress in plants is the measurement of Na^+ or Cl in cotton leaves and roots; it's common to use both the K^+ content and the K^+/Na^+ ratio (Abbas et al., 2010). K^+ level in Arabidopsis decreased after 4 hours of application of 100 mM NaCl (Demidchik et al., 2010). Additionally, because they affect nutrient intake, other studies are conducted on the ratios of other ions, such as Na^+/Ca^{2+}, Ca^{2+}/Mg^{2+}, and Cl/NO_3 (Malik, 2022). The photosynthetic process is also slowed down by salt stress (Liu et al., 2019). While the cotton plant is under salt stress, stomatal conductance, chlorophyll fluorescence, and chlorophyll concentrations are also measured (Hatam et al., 2020). Chlorophyll contents in wheat reduced after three days of salt application (100 mM) (Tian et al., 2015). Osmotic pressure frequently coexists with salt stress, usually established by changes in water potential, relative water content (RWC), turgor pressure, and osmotic pressure (Yin et al., 2013). For instance, tomatoes' water potential decreases after two hours of exposure to 100 mM NaCl (Mäkelä et al., 1998). The ROS is significantly elevated when under salt stress (Shi et al., 2007). Typically, a rise in ROS production under salt stress damages cell membranes (Tanveer and Ahmed, 2020). Thus, electrolyte leakage and water loss are indicators of cell membrane breakdown, another salt stress symptom (Khan et al., 2013). As an illustration, when 100 mM NaCl was applied for two days, electrolyte leakage from the sunflower increased (Aziz et al., 2019).

7. Cotton tolerance to salt stress: Physiological and Biochemical Mechanisms

Salinity stress causes physiological and morphological problems in cotton leading to decrasing its yield (Etesami and Noori, 2019). Plant nutritional and ionic imbalances occur in response physiological and morphological alteration under salts stress (Shahid et al., 2020). The combined effects of salinity stress on cotton plant development, physiological processes, and biochemical features have not been the subject of any meta-analyses (Malik et al., 2022).

Salinity stress often causes cotton plants to produce less biomass (Galić et al., 2020). In numerous investigations, salinity stress was demonstrated to have an additive influence on the buildup of dry matter (Prodjinoto et al., 2021). Some studies claim that shoot length is decreased because salinity raises the concentration of NaCl (Chauhan et al., 2019;Kumar et al., 2021). Varying water stress levels did not significantly impact shoot length, SDW, and RDW (Masuda et al., 2021;Angon et al., 2022). The total amount of assimilates decreased due to the negative effects of salt stress on plant photosynthetic rate and biomass accumulation across the growth duration (Yadav et al., 2019;Raziq et al., 2022). According to research, salt stress drastically lowers the amount of chlorophyll (Bibi et al., 2019;Gerona et al., 2019). However, consistent irrigation is linked to the highest levels of chlorophyll (Khalvandi et al., 2021).

7.1. Osmotic and salinity

The cotton plant maintains its capacity to absorb water through osmotic adjustment, raising its cells' solute content (Hou et al., 2021). Under osmotic adjustment, there are two osmotic correction pathways. One potential is that the solute itself needs to serve as an osmolyte. However, solutes serve as a defence force by preserving the structural integrity of biological macromolecules. This poor attachment of water molecules to the hydrophobic regions of the protein surface, especially in hypertonic circumstances, may be the mechanism underlying the phenomena, in a hypertonic environment, cells initially lose this percentage of water. Proteins' surface polarity can be increased by dissolving osmotic regulators in the water that binds to them, improving the proteins' ability to adhere to water (Schobert and Tschesche, 1978). The two main categories of osmotic regulators are organic compounds and inorganic ions. In reaction to osmotic, these substances will be present in cells to variable degrees.

7.2. Organic Substances

Proline is quite capable of hydrating. Its hydrophilic end can cling to water molecules, while its hydrophobic end can bind to proteins. Proline-linked proteins are better able to bind to water, which protects them against dehydration and osmotic causes proteins to denatured. Plants can increase proline synthesis and decrease proline breakdown to accumulate proline in response to stress (Verbruggen and Hermans, 2008). Proline may also start to function as an antioxidant to stop the oversupply of reactive oxygen species that occurs in reaction to stress. It can assist plants in overcoming stress by playing the role of a quick source of nitrogen and carbon for regeneration (Hayat et al., 2012). It results in some stress-related reactions as a sign of stress. Several studies have found that proline can play significantly role in recovering plants from salinity (Banu et al., 2009;Ahmad et al., 2012). Proline treatments to different cultivars of *Brassica juncea* reduced the adverse effect of salinity on photosynthetic activities leading to improve their growth (Mittal et al., 2012).

Additionally, glycine betaine acts as an osmotic regulator. The enzymes choline monooxygenase (CMO) and betaine aldehyde dehydrogenase oxidize choline to produce betaine (BADH) (Bao et al., 2011). Plants have 12 different types of betaine, with glycine betaine being the most well-known and fundamental (Hafez et al., 2021). To decease the damage, which caused by salt stress, it may promote the integrity of plant cell membranes and enzyme activity. It has been found that many higher plants, especially those in the *Gramineae* and *Chenopodiaceae* families, acquire betaine exposed to salt stress (Flowers and Colmer, 2008). (Gupta et al., 2018), observed an increase in glycine betaine synthesis in halophytic seashore paspalum exposed to salt stress caused by choline. Numerous studies have also shown the benefits of topically administering betaine to plants experiencing salt stress (Hirt and Shinozaki, 2003;Ilyas et al., 2022).

Osmotic regulators can also be made from polyols and soluble carbohydrates. The metabolism of plants depends heavily on non-structural carbohydrates like glucose, sucrose, fructan, starch, and others. In particular, sucrose synthesis is increased when plants are under osmotic stress by raising the activity of sucrose phosphate synthase, which is closely associated with plant development and environmental sensitivity (SPS). According to (Peng et al., 2016), the levels of sucrose and starch increased along with the activities of sucrose phosphate synthase (SPS) and sucrose synthase in the main-stem leaves and subtending leaf bolls of cotton (*Gossypium hirsutum L.)*. Even with a significant decrease in starch synthesis, the sucrose concentration in the plant cells of *Phaseolus vulgaris* may remain stable. Sucrose phosphate synthase activity was reduced by osmotic stress (SPS), but it also greatly reduced the synthesis of starch, allowing sucrose concentration to stay relatively high.

7.3. Inorganic Ions

Most inorganic ions that make up the osmotic pressure in cotyledons' cells are K^+, Na^+, and Cl. K^+ is a crucial element for plant development and it's essential in preventing the effect on plant cells caused by salt stress. Greater plant hydration status led to increased biomass and improved salt tolerance in stressed peanuts after exogenous K^+ treatment, as shown by (Chakraborty et al., 2016)..

In non-halophytes, rapid Cl uptake by plants during the earlier than-usual stages of salt stress elevated osmotic regulation of the root scheme. Moreover, for the final stages of osmotic pressure regulation, Cl still requires Na^+ or K^+. The presence of Ca^{2+} in the cytoplasm is required for signal transduction. Ca^{2+} channels are encouraged to open while plants endure being exposed to salt stress.

Cell metabolism and gene translation are controlled by Ca^{2+} binding with calmodulin or other calcic binding proteins, and this is referred to as a calcic binding protein, plants are better able to adapt to adversity. To put it another way, Plants survive their capacity to accumulate water from their surroundings when they are affected by salt stress by rising the composition of inorganic ions, such as K^+, and organic compounds, Proline and betaine are two examples.

7.4. Antioxidants enzymatic system against oxidation

SOD is the initial line of defence in plants' entire antioxidant enzymatic system against oxidative stress (Ighodaro and Akinloye, 2018). O_2 is dismutase into H_2O. SOD can indeed be divided into CuZn-SODs, Mn-SODs, and Fe-SODs based on the variations in the metal ions that bind to the SOD. Fe-SODs, Mn-SODs, and CuZn-SODs are primarily discovered in chloroplasts, mitochondria, and extracellular space, respectively (Corpas et al., 2006). CuZnSOD was introduced into a salt-sensitive sweet potato by Yan et al. and found using the stress- reflect the actual SWPA2 promoter. Under salt stress, transgenic plants have shown a significantly higher expression level than wild-type (Baghour et al., 2019).

To form phenoxyl radicals (PhO), phenolic compounds (PhOH) must be oxidized by POD. In this process, H_2O_2 acts as an electron acceptor and is then transformed into $2H_2O$ (Gross et al., 2006). POD is present in many different plant tissues. As a high-activity adaptive enzyme, it can show the development and growth of plants, in vivo metabolism status, and environmental adaptation. Research conducted by (Yang et al., 2023), that POD activity enhanced with the aid of AMF (*arbuscular mycorrhizal fungus*) in response to the ROS effect brought on by NaCl treatment.

CAT may break down H_2O_2 quickly, releasing H_2O and O_2. The ability of CAT to reduce oxidative damage is demonstrated by the fact that the better the CAT activity in plants, the lower the H_2O_2 rise ratio. The impact of H_2O_2 pretreatment on maize leaves was investigated by (Bakala et al., 2023). The highest initial activity and the strongest response to H_2O_2 were displayed by CAT, showing the role it plays in plants' ROS scavenging (Jiang et al., 2023).

H_2O_2 can be used as an oxidant in APX to catalyze the conversion of AsA to MDHA. Higher plants' APX enzymes are divided into chloroplast APX and cytosolic APX (cAPX) (chlAPX). Stroma APX (sAPX) and thylakoid-bound APX are chloroplast APX (tAPX) types. Microsomes (peroxisomes, glyoxysomes) and some enzymes whose cytoplasmic locations are still unknown are among the cytoplasmic kinds. The oxidation of AsA to form MDHA and, consequently, DHA, as well as the detoxification of H_2O_2, is processed in which all enzymes can take part. In the AsA-GSH cycle, several enzymes play a part in the process regeneration of AsA and GSH but do not directly interact with ROS (Figure 3). AsA is generated from MDHA by the NADH or NADPH-dependent enzyme MDHAR. To achieve AsA regeneration, DHAR catalyzes the oxidation of DHA (Ding et al., 2023). The AsA-GSH cycle regulates redox homeostasis by converting GSSG to GSH and depends on the enzyme GR. Enzyme GPX may decrease H_2O_2 and shield cells from oxidative effects with the aid of GST by using GSH and thioredoxin. They discovered strong evidence within the research of Gaafar and Seyam to support the AsA-GSH cycle's participation in salt tolerance and the mechanism of Egyptian lentil varieties (*Lens culinaris Medikus*) (Gaafar and Seyam, 2018).

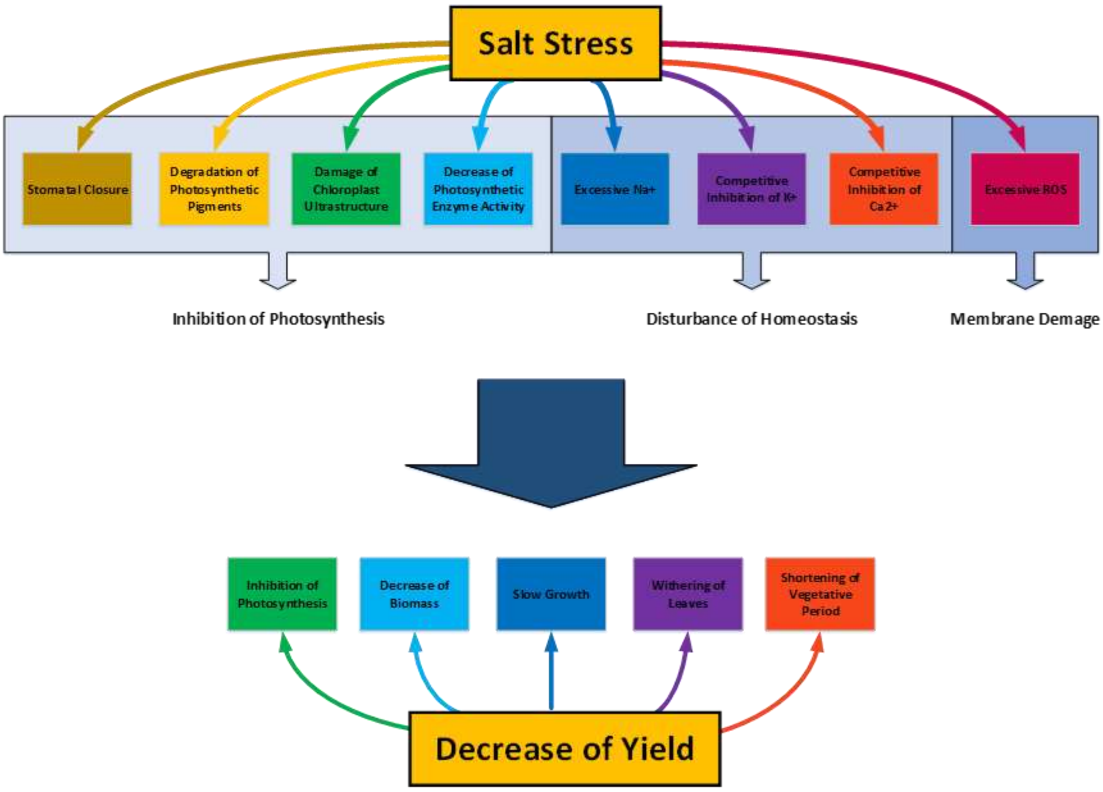

Figure 3. Processes of antioxidant defence Additional information can be found in the text.

7.5. Non-Enzymatic Antioxidants

Active growth regions like meristems, photosynthetic cells, root tips, flowers, and immature fruits are rich sources of AsA, a potent water-soluble antioxidant. Normally, AsA plays a substantial role in scavenging ROS under stress by acting as a co-enzyme and giving electrons. Additionally, AsA plays a role in regenerating the crucial antioxidant tocopherol. Additionally, AsA is regarded as a key signal substance in controlling the redox state of cells and is crucial for the mitochondrial electron transport chain and photosynthetic system (Mittler, 2002). In numerous investigations, Exogenous AsA has been indicated to stimulate plant growth and enhance plant resilience to salt stress. Exogenous AsA, for instance, dramatically increased the development of wheat seedlings when there was a water constraint (Elkeilsh et al., 2019).

Plants can combine lowered glutathione (GSH) and oxidized glutathione (GSSG). Scavenging ROS allows GSH to play a crucial part in controlling intracellular defence. Additionally, as a part of the AsA-GSH cycle, GSH supports redox equilibrium. In the first phase of the AsA-GSH cycle, which uses AsA as an electron donor, APX reduces H^2O^2 to water. MDHAR regenerates the oxidized AsA (MDHA). MDHA, on the other hand, is a free radical that, if not rapidly simplified, is converted to DHA. DHAR converts DHA to AsA at the expense of GSH, a way that results in GSSG. In Jiang DX. *et al*. research, Exogenous AsA, and GSH increased the levels of endogenous AsA and GSH, decreased the levels of H_2O_2 and MDA, and Exogenous AsA and GSH improved the contracts of SOD, APX, and GR in the chloroplasts of two rice cultivars under salt stress, implying that exogenous AsA and GSH may be beneficial for salt stress resistance and ROS scavenging (Jiang et al., 2020).

CAR can be utilized in chloroplasts as supplemental pigments for light collection. Additionally, it can eliminate ROS generated by photosynthesis equipment. CAR security measures the photosystem in a total of four ways: they work with lipid peroxidation materials to stop the chain reaction; they eliminate singlet oxygen and release it as heat energy; they interact with triplet or activated chlorophyll molecules to prevent singlet oxygen formation; and they release extra energy via the lutein cycle. Tocopherol is also a significant ROS scavenger in plants, particularly tocopherol (Ve). To control the stabilization of membrane lipids, it snares ROS and free radicals generated by

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lipid peroxidation. Active oxygen scavengers known as flavonoids have received significant attention in recent years; however, it has been discovered that they only function at the close site of ROS production, like a vacuole or a cell wall. Proline, for example, is an osmotic regulator (Kahraman et al., 2019), and mannitol, also (Ejaz et al., 2020), discovered to have the capacity to scavenge ROS To reduce the harm caused by salinity; plants scavenge ROS using both an enzymatic and non-enzymatic system.

8. Additional Physiological Control in Salt Stress

Ion compartmentation appears to be a universal ability of plants because it occurs in both halophytes and non-halophytes. Halophytes have a different ion separation function than non-halophytes. In most cases, halophytes divide the cytoplasm from the assimilated saline ions in vacuoles, protecting the cytoplasm from the saline ions' toxicity. On the other hand, non-halophytes typically reduce the absorption of potentially damaging saline ions while also transporting The consumed saline ions are transferred to older tissues for capacity, defending young tissues at the expense of older tissues. The transmembrane proteins H^+-ATPase, PPase, Ca^{2+}-ATPase, secondary transporters, and numerous ion channel proteins are required for saline ion compartmentation. To pump H^+ out of the cell and create a transmembrane potential gradient, H^+-ATPase and H^+-PPase on the membrane or vacuolar membrane hydrolyze ATP or pyrophosphate (PPI) to produce energy. The proton pumps-related Na^+/H^+ antiporters and vacuolar membrane then transfer Na^+ into the cell the potential gradient. To lower the osmotic possibilities in the cytoplasm, ions can also be transferred into the vacuole. Na^+/H^+ function is decreased by salt stress, but this effect enhances the amount of unsaturated fatty acids in the cell membrane. The Na^+/H^+ antiporters that ensure Na^+ in the vacuole significantly lower the vacuole's osmotic possibilities and lessen the harm that Na^+ causes to the cytoplasm.

One of the traits of greater plants' salt tolerance is the presence of salt vesicles. It is a type of trichome-derived big, extremely vacuolized cell. Different species have different salt vesicles with different shapes and sizes. Water storage to secure plants from short-term osmotic stress, retrieval of organic osmolytes, collection of ROS scavengers, storage of photosynthetic protein, and so on. A significant portion of the salt vesicle's mechanism has been elucidated, although only at the cellular level. The entire salt secretion process's mechanism must be augmented because it is incomplete. There isn't much research on the formation of salt vesicles at the molecular level. Identifying the essential genes that govern salt vesicle generation has not been possible. It is also important to consider whether the genes connected to those governing salt vesicle development are linked to salt tolerance.

8.1. Ca^{2+}-Dependent Signalling Pathways Pathway

Plant cells experience a rapid rise in Ca^{2+} content while under salt stress. Ca^{2+} has been recognized as a signal molecule associated with the transduction of salt stress signals being an osmotic regulator. Changes primarily influence ca+2 involvement as a second messenger in cell Ca^{2+} concentration. Ca^{2+} input and outflow in plant cells are regulated by various Ca^{2+} channels, Ca^{2+} pumps, and H^+/Ca^{2+} antiporters found on cell and organelle membranes. As a result, cells have the flexibility to control adjustments in Ca^{2+} intensity and concentration and initiate various signalling pathways.

8.2. SOS Pathway

The SOS^3 gene produced a protein that binds Ca^{2+}. To stimulate the action of SOS^2 kinase, the SOS^3 protein can bind to the SOS^2 protein's regulatory area at the C-terminus. SOS^1 is phosphorylated by the activated SOS^2 protein, which consequently increases SOS^1 transporter activity.

As a result, a high external Na^+ increases internal Ca^{2+}, which is the SOS signal transduction pathway. Before binding to SOS^2, SOS^3 initially binds to Ca^{2+}. SOS^3 disables SOS^2 self-inhibition to activate SOS^2 kinase activity. The SOS^1 transporter on the plasma membrane is subsequently phosphorylated by the complicated SOS^3 and SOS^2, improving its capacity to transport Na^+ out of the cell. Another Na^+/H^+ antiporter found on the vacuole membrane is NHX1. It can transport K^+ and Na^+

into the vacuole using a proton gradient. The protein NHX1 controls protein localization, vacuolar pH, K^+ concentration, vesicle trafficking, and the salt response mechanism. SOS kinases control NHX1, which is also controlled by ABA, to control the entry of Na^+ into vacuoles. NHX requires a proton gradient to generate energy during Na^+ transport, the vacuole membrane contains several H^+-ATPase and H^+-PPases to promote Na^+ compartmentation. (Qi and Spalding, 2004) the research found that the SOS^3 is unnecessary for the procedure that moves Na^+ into vacuoles. The SOS^3 homologous protein ScaBPs can also fulfil the same function.

8.3. CDPK

Cotton plants have several Ca^{2+}-dependent protein kinases (CDPKs). Both membrane-bound and membrane-free cells have CDPKs, depending on their subcellular location. They are engaged in both the process of resistance to abiotic stress and control throughout the entire plant cycle of growth and development. In general, accepted that CDPKs primarily control the stomatal and the expression of genes associated with ion channels to control plant resistance to salt stress. The protein kinase and other downstream signalling components are activated by the signal transduction transcription factors that the CDPK genes decode in various plants. CDPKs can control the equilibrium of ROS by controlling the expression of NADPH oxidase and encouraging the synthesis of antioxidant genes, contributing to the responding to oxidative stress and enhancing plants' tolerance to salt.

8.4. Ca^{2+}- (MAPKs Cascade)

Protein phosphorylation mediated by protein kinases, MAPK cascades can gradually increase plants' environmental signal transduction pathway, which is one of the most significant. It can transmit a signal to the cell's DNA in the nucleus from a receptor on its surface. To control plants' physiological responses to salt stress, there is an intricate network made up of multiple stress-inducible signal pathways. The only four pathways that we are more familiar with and have more significant roles are the SOS, ABA, CDPK, and MAPK pathways. In recent years, more elements of salt stress signal transduction have been found and characterized, several questions still need to answer. There is still much to learn about the selectivity and interactions of salt-stressed plants' many signal transduction pathways. Future research should also focus on how different abiotic pressures alter signal transduction networks, and how different signals interact with one another when several abiotic stresses are present.

9. Genes Involved in Salt Tolerance

A molecular process supports plants' physiological ability to tolerate salt. In higher plants, genes involved in osmolytes, autoxidation, ion transport, signal transmission, and regulatory functions are the main subjects of salt-responsive gene experiments, according to Figure 5.

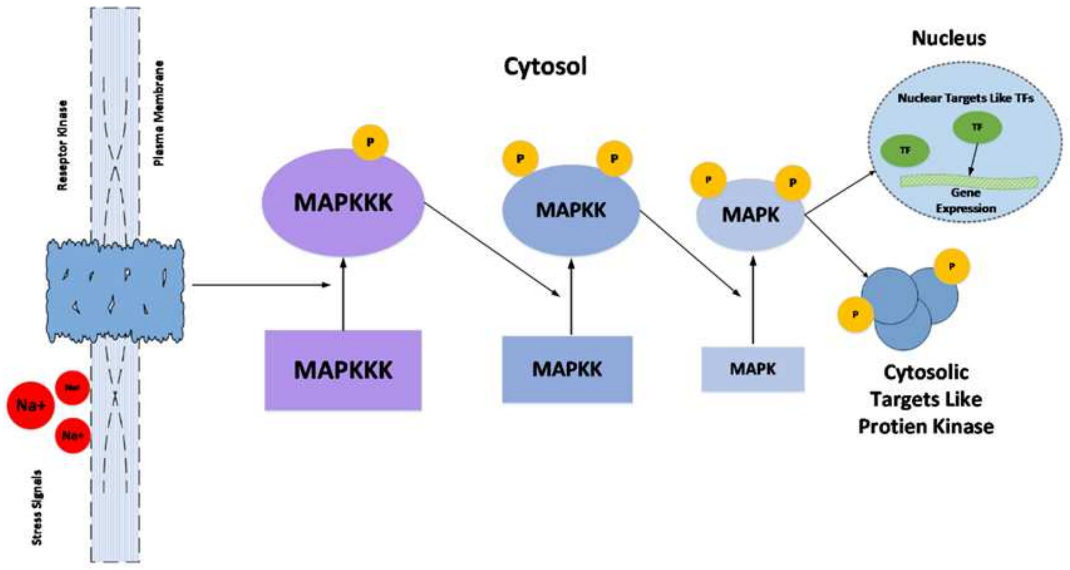

Figure 4. The MAPK cascade's mode.

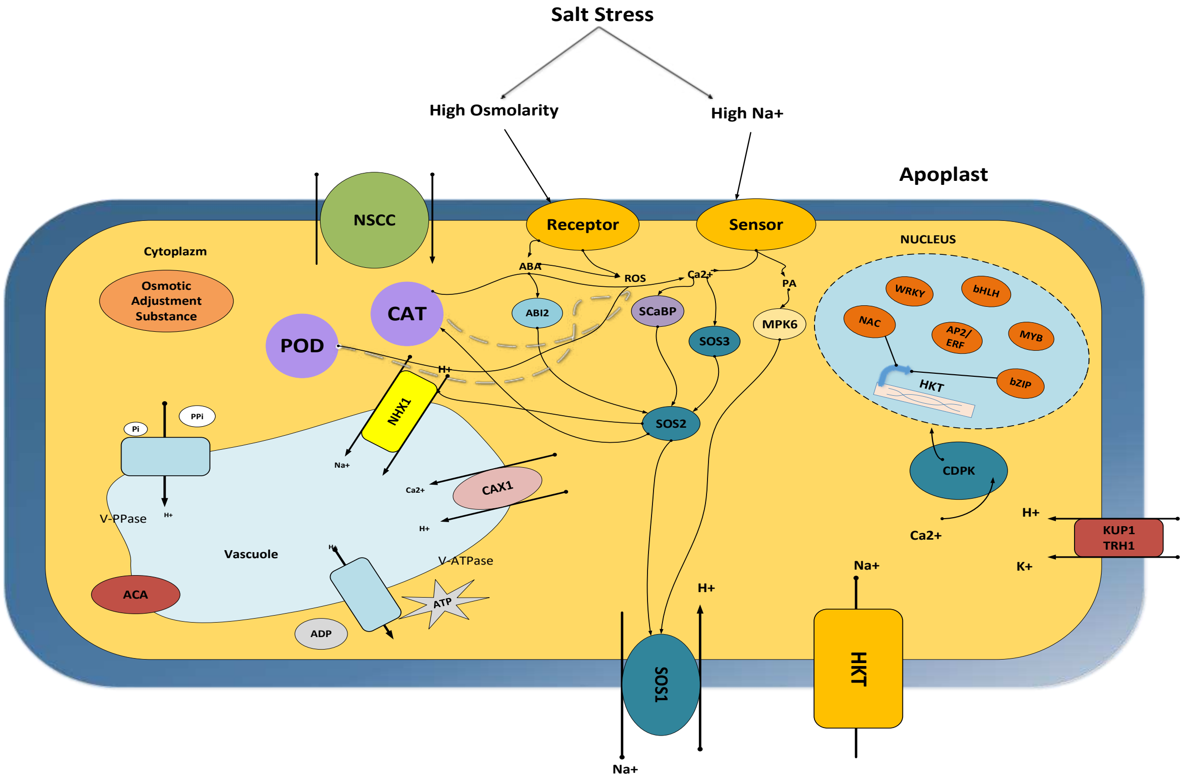

Figure 5.

9.1. Genes Involved in Osmotic Adjustment

Plants that are stressed by the salt can collect molecule solutes or osmotic agents. Osmotic regulators, including proline, betaine, treehouse, mannitol, fructan, and glycogen, can be produced by plants when they are under water stress since osmotic regulator synthase genes have been inserted into their genomes. Plants currently have defined metabolic routes for proline. The Glu and Orn pathways are the two processes plants use to synthesize proline. Both Glu and Orn are the first substrates. Some essential rate-limiting enzymes control each process. The Glu pathway's key enzymes are 1 pyrroline-5-carboxylic acid synthetase (P5CS) and glutamate dehydrogenase (GDH);

the Orn pathway's key Ornithine aminotransferase (OAT) and arginase are examples of enzymes. The main enzyme involved in the breakdown of proline is proline dehydrogenase (ProDH). For example, Chen *et al.* proposed that proline was produced excessively and salt tolerance was increased in transgenic Arabidopsis thaliana when P5CS1 and P5CS2 cDNA were introduced. In plants, two stages of enzyme processes are primarily responsible for synthesising glycine betaine. Choline is initially converted into betaine aldehyde by an oxidation reaction that CMO catalyzes. Wang et al. observed that the Suaeda liaodonggensis was used to clone the BADH gene, which was then introduced into tomato (Solanum Lycopersicum). Additionally, the soybean was revealed to contain the unique tonoplast intrinsic protein GmTIP2, which may be crucial for osmotic control.

The biosynthesis of sucrose is a challenging process. 1, 6-diphosphate fructose (FBP) and sucrose phosphate synthase are the key rate-limiting enzymes in the synthesis of sucrose (SPS) (Li et al., 2012). Under salt stress, three differentially FBP proteins were discovered using two-dimensional electrophoresis and internal peptide sequence analysis. According to the findings of this study mechanism through which mangrove plants withstand salt involves FBP.

Plant salt tolerance is closely linked to HKT, a Na^+ or Na^+-K^+ transporter. It can reduce the amount of Na^+ in the shoot, discharge extra Na^+ into the surrounding parenchyma cells, and maintain K^+ homeostasis in vivo. HKT proteins can be split into two categories based on the distinct ways that Na^+ and K^+ are transported in the heterologous expression system: When the external K^+ level is low, HKT1 primarily affects the transport of Na^+ and mediates Na^+ absorption; HKT2 serves as a K^+-Na^+ cotransporter (Noble and Rogers, 1992). Han et al.'s study on wild barley in Tibet revealed that HvHKT1; 1 knockdown caused Na^+ accumulation in roots and leaves. When HvHKT1; 1 was overexpressed in salt-sensitive Arabidopsis hkt1-4 and sos1-12 mutant strains, Na^+ content in root and shoot was significantly reduced, demonstrating that HVHKT1; 1 is important for Na^+ transfer in roots. However, recent research found that HvHKT1; 5 knockdown barley lines had much higher K+/Na+ ratios than the wild type and significantly less Na^+ translocation from root to shoot. In contrast to other HKT1; 5 members, HvHKT1; 5 exhibits salt tolerance is negatively regulated, this clearly shows that barley has a different Na^+ transport mechanism. Zhang, Y., *et al.* Yao, X., *et al.*, and Kader, M.A., *et al.*, found that under salt stress, Rice transporter genes OsHKT1, OsHKT2, and OsVHA were engineered to express and were found to be capable of lowering Na^+ content by regulating the Na^+/K^+ ratio.

9.2. Genes Involved in Antioxidants

A significant amount of ROS is produced because of salt stress. ROS can be rapidly eliminated by enhanced expression of antioxidant enzyme genes like SOD, CAT, POD, and APX. The variable expression of numerous plant antioxidant enzyme gene families under abiotic stress in the recent period, there has been much research. Ma, Li, *et al.*, carried out the Brassica juncea and Brassica oleracea genome-wide classification and identification of the abiotic-stress-responsive SOD gene family in Rapa. Wu et al. observed through classifying and evaluating Cassava's class III POD gene family's expression. Wang *et al.*, found in Cotton's CAT gene family: genome-wide classification and bioinformatics analysis. Tao et al. implemented the Gossypium hirsutum APX gene family expression profiling and genome-wide analysis.

Other genes are associated with antioxidants in introducing the families of genes encoding antioxidant enzymes. Additionally, significant antioxidants in plants are AsA and GSH. Through the AsA-GSH cycle, they are capable of synergism and renewal. We can increase the production of AsA and GSH by overexpressing crucial enzymes in this cycle, which would increase plants' resistance to oxidative stress. Glutamate cysteine ligase (GCL) first catalyzes the formation of γ-glutamylcysteine from Glu and Cys, and then glutathione synthase (GS) catalyzes the structure of GSH from Glycine and γ-glutamylcysteine [164]. APX helps to detoxify H_2O_2 and oxidizes AsA to deliver MDHA. MDHA can also spontaneously transform into DHA or AsA with the support of MDHAR. DHAR further converts DHA to AsA. Other significant enzymes comprise GR, GSTs, etc. For example, Horváth *et al.* found that AtGSTF8 and AtGSTU19 play a role in fine-tuning redox homeostasis, contributing to Arabidopsis salt stress resistance. 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 varied synthesis pathways uses a different enzyme. Sun et al., experiments in transgenic Arabidopsis, drought and salt stress tolerance are improved by overexpression of the Cerasus humilis ChVDE gene, which encodes a violaxanthin de-epoxidase.

9.3. Plant reaction to salinity stress in genes upregulating and downregulating

Plants use various techniques to either upregulate or downregulate the transcription of genes in reaction to salinity (mRNA) (Table 1). A new strategy in salt tolerance involves several regulators in genes through core dogma, transcription preparation to the participation of TF engaged in the creation of mRNA and protein produced. Salinity alone generates two types of stress in plants: first, it lowers the soil's water potential, which lowers water intake, and increases osmotic and drought stress. Second, it results in an ion buildup that results in ionic stress Nongpiur *et al.* In responding to salt, several genes in plants are stimulated to produce proteins, amino acids, carbohydrates (CCOMT, SAM, GAPDH, AND LAX AP2/ERF), sugars (SWEET15), and proteins (catalase, CAT; glutaredoxin, GRXC1; glutathione-S-transferase, GST), Zhao, W., *et al.,* a significant number of transcription factor genes that is either up or downregulated are reliable with the development of a sophisticated signal transduction system that underlies the reaction to salt stress (Wang *et al.,* 2019).Different plants identified with salt stress have distinct up and downregulated genes (Table 2).

Table 1. Different plants identified with salt stress have distinct genes that are upregulated and downregulated.

Name of Genes	Function	Upregulated/ Downregulated	References
ETR1/ ETR2/ EIN4	Increase salt tolerance	Downregulated	(Arif et al., 2020)
B-ARR, CRE1	Improve plant development with ion homeostasis	Downregulated	(Song et al., 2014)
LHC	Adapt the light-harvesting system	Downregulated	(Ansari et al., 2022)
BRI1/2	Ion homeostasis improves plant development	Downregulated	(Brenya, 2020)
MPK3, MEKK2	Ion homeostasis, osmoprotectant	Downregulated	(Billah et al., 2021)
NPR1	Reduce the input, exclusion, and sequestration of salt	Upregulated	(Bor and Özdemir, 2018)
GmST1	Exclusion of salt and improvement of the immune and antioxidant systems	Upregulated	(Kaushal, 2020)
SAUR, ARF	Promotes plant growth and balance	Upregulated	(Zhao et al., 2022)
CaM, CDPK, CML, CBL	Ion homeostasis enhances plant development and growth	Upregulated	(Shah et al., 2021)
MYC2, TGA	Increase the production of jasmonates and activate plant defenses	Upregulated	(Delgado et al., 2021)
CCOMT	Promote the biosynthesis of lignin and suberin.	Upregulated	(Yu et al., 2022)
NRT1/PTR, CAX1	Enhance the antioxidant system and control calcium homeostasis	Upregulated	(Mitra, 2018)

SOS3/,SOS2/ CIPK24	Salt exclusion and sequestration	Upregulated	(Mahajan et al., 2008)
SDIR1	Salt exclusion and sequestration	Upregulated	(Zhao et al., 2017)
SDIR1	Salt homeostasis, decrease senescence	Upregulated	(Johnson, 2016)
BAK1	Exclusion and sequestration of salt	Upregulated	(Lin et al., 2020)
NCED	Osmoprotectant, closure of the stomata, development of lateral roots, and salt acclimation	Upregulated	(Wani et al., 2016)
LAX	Vascular development	Upregulated	(Chai et al., 2016)
SWEET15	Modify vacuolar transit and sugar storage	Upregulated	(Zhao et al., 2019)
RCA1, AOX1A	Modulate photosynthesis	Upregulated	(Albaladejo et al., 2018)
LRR-RLK, CRR-RLK,	Plant development and growth	Upregulated	(Wang et al., 2016)
NHX1	Transport of salt from the cytosol to the vacuole	Upregulated	(Graus et al., 2022)
SOS, VDAC	Salt exclusion, ion homeostasis, and homeostasis	Upregulated	(Dong and Wang, 2022)
AtNHX1	Enhanced germination and increased biomass	Upregulated	*(Ren et al., 2022)*
OsNHX1	Enhanced biomass	Upregulated	*(Mansour, 2022)*
GutD	Enhanced biomass	Upregulated	*(Khan et al., 2022)*
BADH	Better resiliency to salt stress and development	Upregulated	*(Chen et al., 2022)*
AtNHX1	Improved germination and increased biomass	Upregulated	*(Deng et al., 2023)*
Bt	Improved chlorophyll growth and stability	Upregulated	*(Talaat et al., 2022)*
CAX1	Enhance the antioxidant system and control calcium homeostasis	Upregulated	*(Wei et al., 2017)*
ZEP, ABA 8′- OH, ABI5	Osmoprotectant, closure of the stomata, development of lateral roots, and salt acclimation	Upregulated	*(Bartels and Sunkar, 2005)*

Table 2. Different salt stress genes' roles in different plants.

Gene name	Role in Gene	Origin Gene	References
VvNAC17	An osmotic regulation-related tonoplast intrinsic protein	*Glycine max*	(Yang et al., 2021)
VvNAC17	Increases ABA and stress-related gene expression	*Vitis vinifera*	(Ju et al., 2020)
PpSARK	ABA-related senescence-associated receptor-like kinase	*Physcomitrella patens*	(Li et al., 2018b)

AtGSTU19	Effectively fine-tune redox homeostasis at the root	*Arabidopsis thaliana*	(Horváth et al., 2019)
AtGSTF8	A root-level process that fine-tunes the redox homeostasis	*Arabidopsis thaliana*	(Wang et al., 2022)
SlMYB102	A transcriptional regulator of stress reactions	*Solanum Lycopersicum*	(Jia et al., 2021)
ThDREB	A transcription factor that plays a role in stress responses	*Tamarix his pida*	(Yang et al., 2017)
AtMYB20	Negatively controls serine/threonine protein phosphatases of type 2C	*Arabidopsis thaliana*	(Nguyen et al., 2019)
AtWRKY33	Regulated salt responsive gene improved salt tolerance AtKUP2	*Arabidopsis thaliana*	(Rajappa et al., 2020)
AtbHLH122	Enhanced salt sensitivity via controlling the salt-sensitive gene AtKUP2	*Arabidopsis thaliana*	(Singh, 2022)
GmbZIP2	A gene transcription factor that plays a role in the response to salt stress.	*Glycine max*	(Ke et al., 2022)
GhMPK2	MAPK signaling via protein kinase	*Gossypium herbaceum*	(Zhang et al., 2014b)
GhMAP3K40	In MAPK signaling, protein kinase	*Gossypium herbaceum*	(Ashraf et al., 2018a)
ZmMPK5	MAPK signaling via protein kinase	*Zea mays*	(Zhang et al., 2014a)
ZmMKK4	Protein kinase in MAPKs signaling	*Zea mays*	(Kong et al., 2011)
VvMKK4	MAPK signaling protein kinase	*Vitis vinifera*	(Wang et al., 2020)
VvMKK2	protein kinase in MAPKs signaling	*Vitis vinifera*	(Çakır and Kılıçkaya, 2015)
PtMAPKK4	protein kinase in MAPKs signaling	*Populus trichocarpa*	(Sun et al., 2020)
AtCPK12	protein kinase in CDPKs signaling	*Arabidopsis thaliana*	(Hrabak et al., 1996)
AtCDPK27	CDPK signaling involves a membrane-localized protein kinase	*Arabidopsis thaliana*	(Yue et al., 2022)
OsMADS25	A transcription factor that participates in ABA-mediated regulatory pathways	*Oryza sativa*	(Hussain et al., 2021)
OsNAC45	A transcription factor is involved in several stress and ABA signaling responses	*Oryza sativa*	(Zhang et al., 2020)
ChVDE	Violaxanthin de-epoxidase catalyzes the transformation	*Cerasus humilis*	(Sun et al., 2021)
AVP1	Vacuolar H^+ phosphorylase	*Arabidopsis thaliana*	(Solebo, 2021)
TaTVP1	Vacuolar H^+ phosphorylase	*Triticum aestivuml*	(Hao et al., 2021)

PtVP1.1	vacuolar H$^+$ phosphorylase	*Populus trichocarpa*	(Gao et al., 2022)
VrNHX1	Na$^+$/H$^+$ vacuolar antiporter	*Vigna radiata*	(Bai et al., 2023)
P5CS1	A protein that regulates the rate of proline biosynthesis	*Phaseolus vulgaris*	(Hosseinifard et al., 2022)
P5CS2	The enzyme responsible for limiting the rate of proline biosynthesis	*Phaseolus vulgaris*	*(Chen et al., 2010)*
LrAMADH1	Betaine aldehyde to betaine converting catalyzed	*Lycium ruthenicum Murr*	(Liu et al., 2018)
SlBADH	Promote the transformation of betaine aldehyde to betaine	*Suaeda liaodonggensis*	*(Li et al., 2003)*
AtTPPD	The dephosphorylation of trehalose 6-phosphate to form trehalose is instigated	*Arabidopsis thaliana*	*(Krasensky et al., 2014)*
HvHKT1;1	When the external K$^+$ level is low, transports Na$^+$ and mediates Na$^+$ absorption.	*Hordeum vulgare*	*(Haro et al., 2005)*
HvHKT1;5	Negatively transport Na$^+$ in Barley	*Hordeum vulgare*	*(Zhu et al., 2022)*
OsHKT1	Transport Na$^+$	*Oryza sativa*	*(Zhang et al., 2018)*
OsHKT2	Transport Na$^+$	*Oryza sativa*	*(Yao et al., 2010)*
OsVHA	Transport Na$^+$	*Oryza sativa*	*(Kader et al., 2006)*
AtNHX1	Vacuolar Na$^+$/H$^+$ antiporter	*Arabidopsis thaliana*	*(Sottosanto et al., 2004)*
LfNHX1	Na$^+$/H$^+$ vacuolar	*Leptochloa fusca*	*(Rauf et al., 2014)*

9.4. Genes Related to Signal Transduction

Previous research has related six genes in the Arabidopsis SOS gene family to salt tolerance, either directly or indirectly. Controlling SOS^1 on the plasma membrane, SOS^3 and SOS^2 found in the cytoplasm can control K$^+$ and Na$^+$ ion homeostasis, improving salt tolerance. SOS1 is a SOS family gene directly linked to plant salt tolerance. Under salt stress, it regulates the activity of SOS1 and ion transporters, as well as the growth of root hair, SOS^4 improves salt tolerance. The SOS^5 protein, which is situated back side of the plasma membrane, contributes significantly by fostering the formation of cell junctions and cell walls. SOS^6 is crucial for controlling oxidative and osmotic stress in cells. Simultaneously, significant advancement has been made in locating SOS gene families in different plant species. Dong, X. and his collaborators found the identification of SOS family genes across the genome and study of their gene expression in tuber mustard (*Brassica juncea var. tumida*). Zhao *et al.* observed that SOS family genes from spinach had been identified and characterized (*Spinacia oleracea*).

Protein kinases, particularly CDPKs and MAPKs, are crucial signal transducers that regulate how plants react to abiotic stress. Many plant species have had their CDPK gene families found and investigated (Li et al., 2022b). Interacting with CAT^3 and phosphorylating its 261st serine residue, At CPK8 modulates the activity of CAT^3 and, in turn, the capacity of plants to scavenge ROS. MAPK members involved in response to salt stress have been identified in some plants over the last few decades (Sadau et al., 2022). As a result of severe salt stress, AtMEKK1 in Arabidopsis phosphorylates AtMKK2 and AtMEK1 to activate downstream kinases AtMPK4 and AtMPK6. Sun, H., *et al*. claimed that Populus trichocarpa PtMAPKK4 overexpression improves tobacco's ability to salt. Based on research conducted by Wang et al., when the grape VvMKK2 and VvMKK4 genes were overexpressed in transgenic Arabidopsis thaliana, seedling development under stress conditions outperformed the wild type. Although overexpression of VvMKK4 only increased tolerance to salt stress, overexpression of VvMKK2 raised response to both drought and salt stress in Arabidopsis. Overexpression of genes

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such as maize ZmMKK4, Khan, M.N., *et al.* Chen, Y., *et al*., and Talaat, N.B., and others can improve transgenic plants' ability to withstand high salt and alkali concentrations.

9.5. Regulatory of several Genes

Salt tolerance is a quantitative genetic trait that involves multiple genes. In reaction to salt stress, transcriptional factors change gene expression to control gene levels. Core transcription factor families, including bZIP, WRKY, AP2/ERF, MYB, DREB, bHLH, CBF, and NAC, have been identified. In hairy soybean roots, GmbZIP2 may be responsible for the overexpression of stress-responsive genes such as GmMYB48, GmWD40, GmDHN15, GmGST1, and GmLEA. Transcription factors bHLH and WRKY contribute to Arabidopsis thaliana's enhanced salt tolerance by managing the expression of the salt-responsive gene. According to Nguyen, N.H., *et al.* (2019), controlling ABA signalling pathways, AtMYB20 in Arabidopsis thaliana influences plants resistant to salt stress for sale. ABI1, ABI2, and AtPP2CA gene expression levels decrease under salt stress when the AtMYB20 gene is overexpressed, which enhances transgenic Arabidopsis' resistance to salt stress. ThDREB transcription factor can increase Tamarix hispid's ability to tolerate salt by continuing to increase the antioxidant enzyme's activity. According to research by Chen, J. *et al*., In Arabidopsis thaliana, overexpression of VvNAC17 increases plant tolerance to salinity and drought through enhancing the expression of ABA and stress-related genes such as ABI5, AREB1, COR15A, COR47, and P5CS.

In addition to transcription factors, some regulatory genes are linked to plant salt tolerance. Numerous short non-coding RNAs, such as microRNAs (miRNAs), have emerged in recent years as crucial regulators of chromatin remodelling, translation inhibition, and mRNA degradation MiRNA targets include the metabolic pathway, the ubiquitination pathway, transcription factors, signal transduction elements, and genes concerned in RNA manufacturing and protein synthesis. Transgenic Osa-miR393a increased K^+ uptake and salt stress tolerance compared to wild-type controls.

Although recent advances in research on the plant genes attributed to salt tolerance, it is still primarily concentrated on locating and modifying the homologous genes responsible for salt tolerance in Arabidopsis. Finding new salt-responsive genes can be done with an appealing approach. Comparative genomics or transcriptomic analysis can be used to investigate halophytes and find new salt-responsive genes. For instance, using transcriptome analysis, discovered a few more salt-tolerance genes in the halophyte A triplex canescens; although a complete genome is required for a comparative genomic and transcriptomic study, it is expected that as sequencing technologies advance, more and more genome sequences will become available, This will be useful for molecular breeding in the coming years.Different salt stress genes' roles in different plants (Table 2) .

10. Techniques for Non-Genetic Improvement

Traditional breeding is a successful strategy for increasing a plant's tolerance to salt. Recurrent crossbreeding, selective breeding through artificial means, cutting, grafting, tissue culture, and other forms of asexual proliferation are among the techniques used (Suman, 2017). New salt-tolerant plant genotypes can be created. Applying exogenous chemicals can also help plants be better able to withstand salt stress ; exogenous substances are classified as follows: Those that act as osmotic regulators, like betaine, sugar, organic acids, and gibberellin, and those that do not; those that promote plant growth; and those that lessen cell membrane permeability, like salicylic acid, humic acid, and Ca^{2+}. Other examples include those that stimulate the interaction of antioxidant enzymes in plants, like NO, silicon, selenium, and others; those that can act as osmotic regulators. For instance, under conditions of salt stress, plants treated with exogenous melatonin showed higher antioxidant enzyme activity, higher rates of photosynthetic activity, lower rates of electrolyte leakage, and lower MDA contents than the control group; Melatonin suggests improved plant salt resistance by improving photosynthetic capacity, oxidation resistance, and ion homeostasis (Rajput et al.). Another recent approach has been to increase plants' tolerance to salt through the relationship of fungi and roots to create symbionts with specific cells and characteristics. In their study, (Azad and Kaminskyj, 2016;Hao et al., 2021), the influence of systemic fungal endophytes isolated from naturally developing

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plants in determine soil on plant salt tolerance. Compared to non-colonized plants, endophyte-colonized plants had higher root and shoot biomass, better water usage efficiency, higher photosynthetic efficiency, and lower ROS levels (Dastogeer and Wylie, 2017). The harm caused to plants by salt stress can also be effectively reduced through rational fertilization. For instance, phosphorus fertilizer increased Phaseolus Vulgari's ability to tolerate salt.

Genetic Improvement Techniques

Genetic engineering is the most straightforward and efficient way to increase the tolerance of plants to salt, which introduces genes relevant to salt stress into the plant (Shahbaz and Ashraf, 2013). In addition to the genes mentioned earlier, the tobacco osmotin gene has recently received much attention for its potential to help plants under salt stress. Plants react to biotic and abiotic challenges by applying stress-responsive protein osmotic widely. It is a member of the PR-5 pathogenesis-related protein family. It protects plants by preventing lipid peroxidation, initiating programmed cell death (PCD), rising proline content, and enhancing antioxidant enzyme activity. as stated by the researcher, overexpressing the tobacco osmotin protein in transgenic plants protects from a variety of stresses, fungal infections, and salt stress (Das et al., 2011). Xu, Fang, *et al.* found that the putative transgenic chili pepper plants' morphology resembled wild-type plants but were more salt tolerant (Xu et al., 2012). They overexpressed the osmotic gene. Soybeans exhibited the same results in plants with overexpressed tobacco osmotin gene. (Bashir et al., 2021) have researched whether increasing the tobacco osmotin protein in Olives to increase salt tolerance has anything to do with the transgenic plants' sulfur metabolism. Although there is some evidence that the tobacco osmotin protein contributes to increased plant stress resistance, the full mechanism underlying osmotin activity is still unknown and needs to be clarified.

There is a complicated network of levels and plants have genes that help them tolerate salt. Using a single transgenic technique, like upping a specific osmolyte's concentration or a particular oxidase's action, plants' ability to tolerate salt can be increased. The degree of progress is constrained, though. As a result, we must determine how to prioritize each tactic. When significantly raising a plant's resistance to salt, it's best to prioritize our strategies to obtain better results.

11. Conclusions Future Research Perspectives

In our review, we discussed what occurs to cotton plants under salt stress and the physiological reaction that emerges, which involves four primary signalling pathways, the related genes that respond to salt stress, and a few methods for boosting plants' resistance to salt. The main components of the physiological response are osmotic adjustment and ROS scavenging.

Because phenotyping is difficult because of the complexity of stress conditions, which are impacted by genes with small and variable impacts and environmental elements, it is unclear what genetic factors contribute to these tolerances. But salt stresses harm physiological, biochemical, and molecular processes, ultimately preventing cotton from growing and developing normally. Some examples include reduced photosynthetic rate, plant height, leaf and root size, biomass, economic yield, yield components, and inferior fiber quality. Because of this, regardless of whether cotton is grown in a greenhouse or a field (based on yield, components yield, and fiber quality), it is possible to screen it for salt tolerance (according to plant height and biomass).

Many researchers have conducted experiments over the last few decades to understand better the mechanism that regulates plant salt tolerance. Nevertheless, future research and discoveries still have a lot of room. It is not yet clear how salt stress affects plant photosynthesis. The development of salt-tolerant cotton cultivars offers a practical management approach to cotton under salt stress. When selecting cotton genotypes that are salt tolerant, increase Ca, Na, and K/Na ratios utilized with classification factors. The existing genetic diversity could be effectively used to create salt tolerant genotypes. Because QTLs control salt tolerance genetically, marker-assisted classification is an exciting method for indirectly selecting salt-tolerant genotypes. So far, no mutual understanding has been reached. Second, further research is necessary to integrate to identify plant stress, and morphological, physiological, and molecular methods are used. Thirdly, the specific salt-tolerance mechanisms used by halophytes, like salt vesicles, are still largely unknown. Fourth, there is still much to learn about how plants react to salt stress, and it is not yet clear how various signal transduction pathways interact with one another. Fifthly, In the future, comparative genomic and transcriptomic approaches may be more important in identifying genes that respond to salt stress. Finally, we must determine how to prioritize each improvement strategy to achieve better improvements. Overall, Understanding the mechanism underlying plant salt tolerance will take a lot of additional work. Future research should concentrate on the molecular interactions between and within cells that contribute to the response to salinity stress.

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