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Biochemical Mechanisms Regulating Salt Tolerance in Plants

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ABSTRACT:

Damage from nutritional imbalance, osmotic stress, particular ion toxicity, or a combination of these factors results in salinity, which in turn affects plant improvement, growth, and physiological and biochemical activities. The impacts of salt stress on photosynthesis vary greatly among plants. Plants growing in salinity stress experience both ionic & osmotic stress, which increases the buildup of ROS and causes secondary stresses that eventually result in oxidative damage. However, among the ROS are the extremely reactive molecules OH, along with additional species like H_2O_2, and $O_2^{\bullet}$. Moreover, the most potent ROS implicated in the oxidative degradation of biological substrates, including carbohydrates, is $^{\bullet}OH$. Mechanisms of salt adaptation that lead to improved long-term salinity tolerance may employ either the gene products from short-term salt stress or other means for increased resistance. It is likely that enhanced salt tolerance is achieved by the enhancement, activation, or maintenance function of physiological systems that are particularly sensitive to disruption by amplified concentrations of salinization. The mechanism of enhanced tolerance for salinity stress conditions can be associated with an accumulation of enzymatic & non-enzymatic activity in addition to a higher accumulation of indirect sources compared with direct sources.

Keywords: Plant, Salt Stress, Oxidative Damage, Antioxidant Enzymes, Tolerances

1. INTRODUCTION

Salinity challenges may become worse in non-saline soils. It is believed that the main factor limiting plant productivity is salt stress. Salinity causes physiological and biochemical dysfunction, which has a variety of implications on plant development, particularly for glycophytes. Plants have developed a number of defenses against salt stress by balancing cellular hyper-osmolarity and ion disequilibrium [1].

Significant harm is caused by salt stress, particularly ion toxicity stress (mostly from Na^+ & Cl^- ions) that causes generative stress and osmotic effects that reduce water absorption. ROS including hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), and hydroxyl radicals ($^{\bullet}OH$) are produced uncontrollably as a result of oxidative stress. Important biological molecules like RNA, DNA , enzymes , and proteins are oxidatively damaged by these unstable compounds [2], which harms plant productivity and growth. Changes in physiological reactions and metabolic pathways may result from salt stress [3].

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In saline situations, plants typically have two main .problems First an excess of salt in the soil ruins the integrity of metabolic processes and lowers the osmotic potential of soil water, which results in reduced absorption of water and a scarcity of water for plants [4]. In a study by Ashraf [5] damage from nutritional imbalance osmotic stress, specific ion toxicity, or a combination of these factors results in salt, which in turn affects plant growth, improvement, biochemical and physiological activities. Salinity stress influence on photosynthesis varies greatly among plant species [6].

Mechanisms of salt adaptation that lead to improved long-term salinity tolerance may employ either the gene products from short-term salt stress or other means for increased resistance. Enhanced salt tolerance is likely achieved through the enhancement, activation, or maintenance of the function of physiological structures that are particularly sensitive to disruption by amplified concentrations of salinization [7]. The mechanism for plants to protect themselves from oxidative damage under salt stress involves many non-enzymatic and enzymatic antioxidants. The production of antioxidants under these conditions varies not only from species to species but between cultivars of the same species, as well as organ to organ in the same cultivar. Applications of biotechnology that are beneficial for abiotic restrictions by these plants demand real biological data about the target crop species as well as its mechanism's necessary resistance/tolerance to abiotic stresses [8]. More protection against salt stress results from genotypes that can concentrate antioxidant enzymes, which can detoxify ROS more effectively [9].

This article reviews and compiles information on the stress caused by NaCl and improved growth, relative water content, proline, antioxidant enzymes , leaf , electrolyte leakage , and photosynthetic pigment concentration. Proline content, electrolyte leakage, and the activity of antioxidant enzymes (POD, SOD, and CAT) were all elevated by NaCl. This review will therefore increase our comprehension of the mechanisms and occurrence of biochemical characterization of plant tolerances.

2. CLASSIFICATION OF SALTS (TYPE OF SOIL AND DEGREE OF SALINITY)

There are two types of salt stress: primary & secondary salts. The phrase "primary salts" refers to the long-term accumulations of salinity on the soil surface caused by natural processes, such as the accumulation of salts in the ocean transported by wind,water , or rock weathering. Human actions are the primary cause of secondary salinization, with the use of saline irrigation water and land clearing being the most significant [10]. Mian [10] also reported that the physical state of the soil, its pH, its EC , and its proportion of exchangeable sodium are used to categorize salt soil as sodic, saline-sodic, and saline soil (Table 1).

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Table 1. The soil's salinity

Type	Physical State of the Soil	pH (Soil)	EC (dS m^{-1})	Exchangeable Sodium Percentage
Saline Sodic	Normal	< 8.5	> 4.0	> 15
Saline	Normal	< 8.5	> 4.0	< 15
Sodic	Poor	> 8.5	< 4.0	> 15

< = less than , > = greater

Source: Mian [10]

One definition of soil salinity is the rise in ions of sodium (Na^+), soluble chloride (Cl^-), calcium (Ca^{2+}) , bicarbonate (HCO_3^-) , and sulfate (SO_4^{2-}) in soil that influences the growth and development of plants [12]. Salinity is measured by using EC. Salinity Laboratory Staff [11] reported that if the soil's EC surpasses 4 dS m^{-1}, the SI unit of EC (dS m-1) , the soil is considered saline. Katerji et al. [13] and Amirjani [14] found that at 25 °C, soil with an EC of the ECe of 4 dSm^{-1} or 40 mM NaCl or above is considered salinized. Even when the soil ECe is less than 4 dS m^{-1}, the majority of vegetables and cereal crops are extremely vulnerable to soil salts.

3. EFFECT OF SALT STRESS ON PLANTS

Salinity is thought to be the primary factor limiting plant productivity. Salinity causes physiological dysfunction, which presents several difficulties for plant development, especially for glycophytes [15]. Similarly, it is regarded as one of the major obstacles to the crop's global cultivation, particularly in dry and semi-arid regions [16]. Different plant species have different effects of salinity on photosynthesis [6]. The increased concentration of Na^+ reduces K^+ approval and Cl^- reductions in nitrate (NO_3) acceptance under conditions of salt pressure [17].
Several plant species exhibited the accumulation of other organic solutes, such as soluble sugars, under salt conditions [18]. By accumulating certain solutes, such as proline and soluble carbohydrates, plant cells reduce their osmotic potential when exposed to high salt pressure [19]. Under stressful conditions, salt significantly increases soluble sugars; hydrolytic enzymes start the breakdown of starch into sugars. According to current understanding, carbohydrates contribute to the stability of membrane erections and serve as osmotica, or protect certain macromolecules [20].

4. PLANT ADAPTATION UNDER SALT STRESS CONDITIONS

Many biochemical and molecular strategies are used by plants to defend themselves from the negative effects of salinity stress. Salinity-tolerant types showed less inhibition of the conversion of soluble carbohydrates to starch [21]. Some extremely salt-tolerant plants have sole structures that can actively excrete salts, which typically preserves the cellular tools that aid in salt tolerance to some extent [22]. Plants experience a range of molecular and biochemical processes to deal with the harmful effects of salt under stressed conditions. Various biochemical methods include [23]:

1. Regulation of roots' absorption of ions by shoots
2. The selective accumulation or inhibition of salt ions
3. Production of osmolytes that are suitable
4. Ion compartmentalization

5. Modification of the photosynthetic pathway
6. Modifications in membrane structure
7. Phytohormone stimulation
8. Antioxidative enzyme induction

5. THE PHYSIOLOGICAL BASIS OF SALT TOLERANCE

Three distinct plant species exhibit tolerance or responsiveness to salt, and there are three different kinds of processes behind salt tolerance (1) Na^+ exclusion from leaf blades, (2) Tissue tolerance, and (3) Osmotic stress tolerance [24] (Figure 1).

a. Na^+ Exclusion

Many plant species grow in salty environments. To start , because Na^+ has higher hazardous levels than Cl^-, scientists are concentrating on controlling Na^+ transport and exclusion in plant cells [24]. The ability of plants to lessen ionic stress by lowering the concentrations of the ion Na^+ in the cytoplasm of plant cells is a crucial component of salt tolerance. Along with tissue tolerance, this method involves precise plant control over Na^+ transport as well as down- and up-regulation of transporter expression [25]. Salinity tolerance in cereal crops has been observed by James et al. [26] concerning the exclusion of Na^+ from leaves (Fig. 1).

The last degree of Na^+ absorption by the cells in the root cortex and the strict regulation of net loading of the xylem through parenchyma cells in the stele are the reasons for Na^+ exclusion from plant leaves [27]. Avoiding Na^+ toxicity through roots lowers the amount of Na^+ in the leaves, which reduces toxicity; but , if Na^+ toxicity cannot be avoided, older leaves will die within days or weeks , depending on the species [24].

Cytosolic Na^+ is efficiently excluded by the mechanism of vacuolar Nav/H^+ antiports, which move potentially harmful ions from the cytosol into huge, internally acidic, tonoplast-bound vacuoles. Antiports decrease their electrochemical potential (couple downhill passage of H^+) against its electrochemical potential (uphill movement of Na^+) by using the proton motive force generated by the vacuolar Httranslocatina enzymes ATPase and PPiase [28 ;29].

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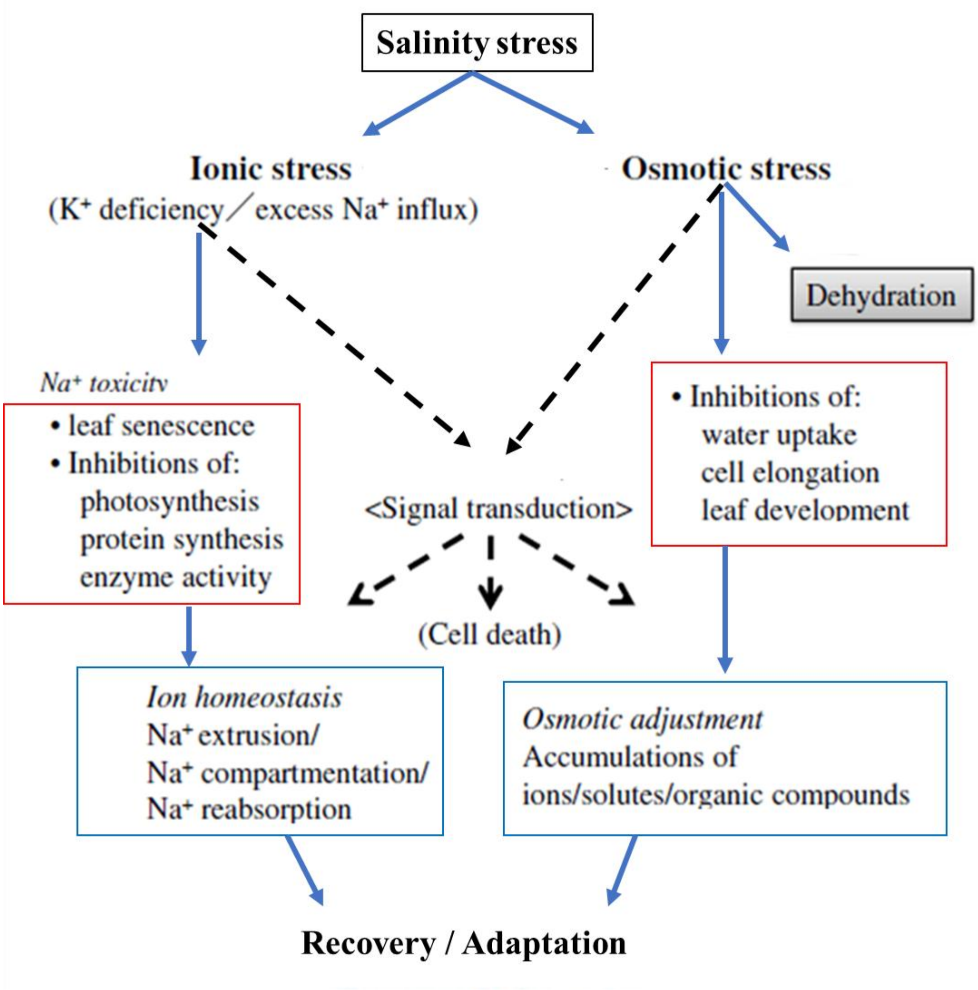

Fig. 1. High salt stress levels harm plant growth, and plants adapt accordingly to withstand these harmful effects. Source: [30]

b. Tissue Tolerance

To improve the survival of older leaves in the second step, plant tissue tolerance is needed. To eliminate hazardous levels within the cytoplasm, especially in the leaf's mesophyll cells, Cl^- and Na^+ must be compartmentalized at the intracellular and cellular levels. As time goes on, toxicity develops when the accumulations of Na^+ in the old leaves reach large levels [24] and the synthesis and cytoplasm contain more suitable solutes. Plant osmotolerance depends on compatible solutes in several ways, including crucial modifications in osmotic adaptation mediating or protective enzymes from stabilizing membranes, denaturation, or macromolecules [31].

The function of suitable solutes, which are usually hydrophilic and not limited to osmotic balance, has also been documented by [32]. These solutes may be able to exchange water at 'membranes or proteins' surfaces. By scavenging ROS, these solutes help to protect cellular structures [33]. Complementary solutes are uniformly neutral, water-soluble, and tiny compounds connected to the disruption of cellular functions, according to [34]. Proline, betaines, sugars, and polyols are among the organic solutes that accumulate in plants as a result of metabolic changes linked to adaptation to such stress [35].

However, glycine betaine plays a role in improving plant resilience to salt stress, even if proline is possibly the most extensively dispersed osmolyte buildup in plants [36]. According to [33], it appears that just a few crop plants and a few halophytes contain glycine betaine.

A common physiological reaction of many plants to a variety of stimuli, together with biotic and abiotic stress, as well as to developmental programs in generative tissues, is the buildup of proline [37]. Due to its capacity to produce ATP for stress recovery, reduce all variables supporting mitochondrial oxidative phosphorylation, and repair damage caused by stress, proline relieves stress [33].

c. Osmotic Tolerance

Osmotic stress causes stomata to close by directly reducing cell growth in plant leaves & root tips. More stomatal conductance and increased leaf growth would result from a reduced reaction to the osmotic stress; however, this enhanced leaf growth would only occur in the presence of sufficient soil water [24].

Regardless of its capacity to keep out salts, the osmotic influence of salinization results in stomatal conductance and slower growth rates, which limits plant growth in salinity conditions [38]. However, according to [25], osmotic tolerance encompasses the plant's ability to sustain leaf growth, withstand the drought-related effects of salt stress, and maintain stomatal conductance.

Relative growth rate and stomatal conductance in plant salinity conditions are positively correlated with the genetic differences in osmotic stress tolerance of 50 worldwide wheat varieties and landraces. High CO_2 levels are linked to high stomatal conductance [38].

However, the older leaves die and the young leaves, which are no longer sustained by photosynthetic export, grow less and produce fewer new leaves if the salinity rises to lethal levels. As a result, the plant receives less photosynthate, which impacts the overall carbon balance that is necessary to promote growth. Accordingly, higher stomatal conductance, enhanced leaf production, and improved growth ability and productivity are all associated with increased osmotic tolerance [24]. This was also maintained by [39] mechanisms of osmotic tolerance in plants associated with stomatal conductance, photosynthetic capability, and water availability to maintain carbon skeletons produced to support the cells' energy requests for growth, which have not been investigated. Finally, the concentration of minerals in the culture media has no bearing on how plants react to osmotic stress.

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6. STRESS FROM SALINITY AND SALT UPTAKE

Soil salinization is a major problem in the production of food because it restricts the use of uncultivated land and limits agricultural growth and expansion. Unlike halophytes, which are native flora of saline areas, the majority of crops are hypersensitive plants or salt-sensitive plants (glycophytes) [40]. Globally, salinity—primarily from NaCl—is the leading cause of crop failure, and significant abiotic stressors lower agricultural yields by more than 50% [41].

Plant progress and growth are harmed by the rise of salt on soil surfaces, also known as soil salinity. Higher toxicity concentrations within cells, osmotic stress, and nutritional interactions and absorption are some of the ways that increased soil salinity affects plants. Salt stress limits rice productivity, as it does for many other crops. The ability of plants to withstand the toxicity of salts is a complicated genetic and physiological characteristic. The physiological mechanisms, ability to sequester otherwise poisonous ions, and anatomy of salinity-sensitive plants (Glycophytes) and salinity-tolerant plants (Halophytes) differ from one another [42]. Plants possess genetic techniques for metabolic and cellular reprogramming that increase the effectiveness of their adaptive mechanisms: (1) modifying signaling and regulatory pathways of the adaptive mechanisms, or (2) directly reprogramming primary metabolism and ion transport processes to confer stress tolerance.

7. OXIDATIVE STRESS

Plants experience osmotic and ionic stress due to elevated soil salinity, which also causes accumulations in ROS production, which in turn causes oxidative stress [43]. When plants are subjected to several forms of stress, oxidative stress occurs [44]. Proteins, lipids, and DNA are all harmed by ROS. Protein oxidative damage causes site-specific amino acid changes and peptide sequence degradation, but cross-correlated response aggregation increases the propensity for proteolysis. Furthermore, ROS can generate a variety of DNA damages that result in mutations, deletions, and other catastrophic genetic consequences [45].

Furthermore, oxidative stress has been shown to be a common plant response to salt stress of biotic and abiotic challenges, such as the buildup and/or production of ROS, which include superoxide anion, hydroxyl radicals, and H_2O_2 [46]. Abiotic stressor conditions due to metabolic issues, ROS , specifically $OH^{\bullet}$, H_2O_2 , and $O_2^{\bullet -}$, are created by aerobic cellular functions, like the chloroplast's electron transport of glucose and xanthine and mitochondria, or the oxidation of glycolate (Photorespiration). Abiotic stressors, such as salinity, increase the production of ROS [47].

Following the production of superoxide toxicity and H_2O_2, they identified a series of reactions that impact the formation of hydroxyl fundamentals and another crucial kind of lipid peroxidase that impedes cellular components and plant processes [48].

Specifically, when the plant lacks defense mechanisms, these ROS are more harmful and can lead to DNA damage, hormone imbalances, lipid peroxidation, nucleic acid oxidation, protein denaturation, and even mutation [49]. The H_2O_2 is a dynamic signaling molecule, and its accumulation (Oxidative stress) results in various dose-dependent cellular responses, as noted by [50], whereas oxidative stress tolerance phases might be a component of the plant's reaction to excessive salinity , they are not anticipated to play a significant role in overall salt tolerance.

Plants have evolved a very effective antioxidant defense mechanism that is composed of both enzymatic and nonenzymatic components to prevent the potentially harmful effects of ROS. This system typically maintains the equilibrium of ROS within the cell [51]. Proline, nonenzymatic

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antioxidants (AsA and GSH) , and antioxidant enzymes (GPX, GR, APX , and SOD) all worked in concert to reduce oxidative stress [52].

8. EFFECTS ON THE YIELD PARAMETERS

Soil salinity affects over half of all irrigated land and 20% of the Earth's land mass, which is the primary cause of abiotic stress in agriculture worldwide. According to [53], increasing the salinity of arable land is expected to have catastrophic global repercussions over the next 25 years, resulting in a 30% loss of land and a 50% loss by 2050. Although rice is the second most important crop in the world and one of the most salt-sensitive crops, in many regions, its production is negatively impacted by salty surroundings [54].

Plants under salt stress are less able to absorb water, which quickly results in a decline in the average growth rate of cell tissues. The flow of assimilates to the plant's developing tissues and meristematic cells is subsequently reduced by the sluggish photosynthetic level process. Another factor that could affect development is salinity. The elder leaves may become more poisonous if the plant is exposed to high concentrations of Cl^- or Na^+. The transfer of growth zones in leaves and carbon compounds to the meristems is further restricted by this damage, which is added to an already reduced leaf area [55].

9. PLANTS' BIOCHEMICAL RESPONSE TO SALINITY TOLERANCE

Salinity stress has a detrimental effect on all kinds of plants. There are several ways that plants have evolved to reduce the effects of salt stress that work to regulate cellular hyperosmolarity and ion disequilibrium. Significant alterations in gene expression cause these processes, which in turn alter plant metabolism. Plants are better able to adjust to disordered metabolic balance thanks to these modifications. The production of metabolites, or plant compounds that aid in plant defense, has been impacted by unfavorable growth conditions [1].

Different changes in gene and protein activity are among the ways that plants react to salt, and these changes always result in changes in plant metabolism. Plants have many metabolic routes that can function well in salt conditions and frequently deviate from the core metabolic pathways at first gene duplication [56].

Tocopherols, glutathione, ASC, and carotenoids are also components of the biochemical defense system. Proline, glycine betaine, and sugars have all been suggested by several researchers to work in tandem with the hydroxyl radical to protect cells [57]. At the maximum NaCl concentration, there is a noticeable increase in proline content and soluble carbohydrates as an osmoregulation [58]. Protein accumulation in salt-saturated plants may contribute to osmotic alteration and provide a nitrogen storage profile that can be utilized later [40].

According to [59], oxidative damage resulted from ion imbalance and hyperosmotic stress. Stressful media cause limited CO_2 fixation, which lowers oxidized $NADP^+$ and carbon reduction via the Calvin cycle, which aids as an electron acceptor in photosynthesis. Through enhanced electron leakage to oxygen, salinity increases the generation of ROS, including $^1O_2$, $RO^\bullet$, $O_2^{\bullet-}$, H_2O_2 and $^\bullet OH$, According to [52], mitochondria can ruin regular metabolism by causing oxidative damage to proteins, lipids, and nucleic acids. Cytotoxic ROS are also produced by metabolic processes in the peroxisomes.

Plant development and productivity are adversely affected by a series of molecular, biochemical, physiological, and morphological changes brought on by abiotic stress [60]. Plants cannot maintain the proper balance of organic components in saline environments, which inhibits growth and productivity. Furthermore, the development factor and ecological factors of plant salt

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uptake vary with ontogeny [61]. Plant systems have strong enzymatic (SOD, MDHAR, POD , GST , GST , GR , CAT , GPX , DHAR , and APX) and non-enzymatic (alkaloids , phenolic compounds , non-protein amino acids, α-tocopherol, GSH, AsA , and ASC) antioxidant defenses that scavenge ROS to prevent oxidative damage and control unchecked oxidation cascades [62].

According to [43], soil salinity buildup causes osmotic and ionic stress in plants, which in turn causes secondary stress by building up ROS products and oxidative stressors. $^{\bullet}OH$, H_2O_2 , $O_2^{\bullet-}$, and $^1O_2$ are among the accelerated ROS products that are a primary indicator of such stress at the molecular level.

Plants that over-express transferred antioxidant genes can be engineered to improve salinity tolerance because antioxidants are linked to higher levels of non-enzymatic metabolites and the production of antioxidant enzymes, which helps to reduce salt stress [5]. Increased salt tolerance results from oxidative stress inhibition, which is corroborated by the overexpression of the protein that transports vesicles and several regulators of antioxidants, including GPX, AAO, and DHAR [61].

According to [52] , rice is more tolerant of salt stress and can produce oxidatives. In contrast, the wild type's accumulation of SOD under salt conditions was not accompanied by GR, GPX, and APX activities, which led to an additional rise in H_2O_2 and the greatest amount of damage under salt stress.

SOD is a member of a family of metallo-enzymes that catalyze the dismutation of $O_2^{\bullet-}$ ions in a two-step reaction that results in the formation of molecular O_2 and H_2O_2 [63]. However, SOD prevents ROS-mediated oxidation of cellular components by catalyzing the dismutation of $O_2^{\bullet-}$ ions into H_2O_2, which is then further metabolized by POD, APX, and CAT. CAT is thought to be more effective than guaiacol-APX and POD because it does not require any decreasing power for H_2O_2 detoxification; however, it has a low substrate affinity [51].

CAT is a tetrameric heme that contains enzymes that may directly dismutate H_2O_2 into O_2 and H_2O. According to [64] , it is essential for ROS detoxification under stressful situations. According to [65] reducing toxic H_2O_2 levels, the observed increase in activity of CAT is believed to represent an adaptive trait that could help overcome tissue metabolic damage.

It is possible that the accumulation of CAT, SOD, and POD activity under salt stress conditions, which are different mechanisms to be an adaptive trait , can help to reduce toxic levels in order to repair the harm to tissue metabolism of H_2O_2 rather than ROS detoxification during stress conditions [66].

10.RESEARCH ON ANTIOXIDANT ENZYMES IN SALT-STRESSED PLANTS

Halophytes' antioxidative response systems (ARS) have been widely cited as having a role in salt uptake [67]. Oxidative stress is fundamentally influenced by salinity and drought. Because of improved stomatal consumption and decreased Calvin Cycle closure of NADPH, accessibility of ambient CO_2 is reduced during salinity-induced oxidative stress. The process known as the Mehler Reaction, which starts sequence reactions that produce more loaded oxygen radicals, may transfer electrons from PS-I to oxygen to form $O_2^{\bullet-}$ when ferredoxin is over-decreased during photosynthetic electron transport [68].

These cytotoxic ROS are continuously generated in the cytoplasm, peroxisomes, and mitochondria during regular metabolic processes. When they are produced in excess, they can impair normal metabolism by oxidatively damaging proteins, lipids, and nucleic acids [69].

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Security features in plant cells can lessen oxidative damage brought on by ROS. The most common method for detoxifying ROS generated during a stress reaction is the administration of ROS-scavenging enzymes that contain APX, CAT, POD, and SOD. The balance between scavenging enzyme activity and ROS production determines the stable-condition levels of ROS in cells of plant [51]. Different plants' ability to withstand salinity depends on their antioxidant defense mechanism [70].

Strong enzymatic ROS-scavenging systems, such as CAT, GR, and POD , are typically found in plant tissues and cells to scavenge ROS. The latter includes DHAR, SOD, APX , and MDHAR. Under salt stress, the coordinated actions of these antioxidant enzymes' different forms in the different cell sections balance the pace of ROS formation and deduction and keep ROS at the appropriate levels needed for cell signaling [24].

High levels of NaCl cause amplified formation of ROS such as H_2O_2, $^{\bullet}OH$, $O_2^{\bullet -}$, and $^1O_2$, and impair electron transport [71]. Plants apply non-enzymatic antioxidants for example ASC and GSH in addition to antioxidant enzymes such as SOD GR, CAT, and APX to scavenge ROS [72].

NaCl stress increases the salt-sensitive wheat genotype's production of H_2O_2, oxygen radicals, especially in leaves, and accumulation of APX in leaves [73]. NaCl stress was applied to two rice cultivars: the salt-sensitive Pusa Basmati 1 and the salt-tolerant Pokkali. In contrast to Pusa Basmati 1, Pokkali exhibited higher amounts of GSH and AsA as well as high ROS-scavenging enzyme activity. However, Pokkali's SOD activity was lower, its H_2O_2 levels were lower , and it had less lipid peroxidation under stress. Additionally, it was discovered to be able to shield the ROS from dangerous cellular constituents. Plants have evolved several detoxification strategies, such as the production of different enzymes and antioxidant compounds [49].

According to [74], both tolerant and sensitive wheat cultivars under salt conditions demonstrated an increase in APX, POD , GR , and CAT activities as salt levels rose.

To test for salt tolerance, two distinct rice cultivars were selected: the salt-tolerant Pokkali and the salt-sensitive IR64. The salt-tolerant (Pokkali) cultivar under salt stress showed a lower level of H_2O_2 and a higher ratio of reduced ascorbate/oxidized ascorbate than the salt-sensitive (IR64) cultivar. Nevertheless, the action was boosted by the methylglyoxal detoxifying system. Furthermore, oxidative DNA damage and ROS levels could be sensitive biomarkers for salinity screening [75].

According to [9], the cell membrane may be protected by APX and CAT activities in conjunction with increased GR and DHAR activities. It was discovered that in salt conditions, the H_2O_2 concentrations were significantly lower in tolerant genotypes. The activities of DHAR, APX, POD, SOD, GR, and CAT, which are essential for detoxifying ROS, could account for 99.8% of the variability in antioxidant enzymes for lowering H_2O_2.

When salt-tolerant rice seedlings were cultivated in 7 and 14 dSm^{-1} NaCl, the activity of CAT, DHAR, GR, GPX, and MDHAR, was shown to be elevated. Additionally, it was demonstrated that the primary criteria for choosing rice types that can withstand salt could be high levels of antioxidants (ASC and GSH) and coordinated, high CAT, GPX, SOD, GR, and APX activities [76].

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11. UTILIZING TISSUE CULTURE IN RESEARCH ON SALT TOLERANCE

An efficient and quick way to understand how plants tolerate salt is by *in vitro* cultivation [77]. The creation of a highly efficient plant *in vitro* regeneration system is necessary for the development of the plant using a number of modern biotechnological techniques, such as breeding via genetic transformation and somaclonal variation. [78].

The ability to cultivate plants from a mature embryo offers many benefits, such as the ability to produce plant material regardless of the season or geographic location, a lower risk of microbial infection, and ease of use. As a result, many plant biotechnology specialists use this method extensively [79].

Tissue culture methods can be used to produce rice somaclone. Organs exposed to physical and chemical mutagenic agents develop mutant callus, which aids in the development of soma clones, salt- or stress-tolerant mutant lines, and disease, pest, and insect resistance in plants. Changing the culture media, especially the plant hormone in the media, explants, the amount of time spent *in vitro*, and the culture techniques might all control the somaclonal variance [80].

Breeders can generate novel crop genotypes by using the *in vitro* approach. Over the past few decades, plant breeders have been using plant tissue culture as a standard practice, which has led to the creation of numerous edible varieties that are grown for food all over the world. More mutations are a necessary component of plant breeding, and the quantity of genetic variety brought about by tissue culture is modest and controllable. Additionally, varieties have thrived in the field with no signs of health issues [81]

12.MICROPROPAGATION

Explants and their subcultures for acclimation, prepropagation, shoot and root growth, and proliferation are the typical phases in the micropropagation technique [82]. A highly efficient *in vitro* plant regeneration technology system must be created in order to improve the crops for a number of biotechnological operations, such as plant breeding via genetic transformation and somaclonal variation [83]. Because the callus has a high potential for regeneration, is readily available throughout the year, and is easy to disinfect, naked seeds were more frequently used as explants for induction callus in rice tissue culture than their origins, such as shoots and roots [78].

Mani alters the ratio of cytokinin to auxin in culture conditions to make somatic embryos, shoots, or roots that can later be used to create whole plants. Additionally, callus culture can be used to start cell suspensions, which are used in studies on plant transformation [84].

However, genetic diversity, or somaclonal variants, may be produced by *in vitro* culture due to changes in epigenetic markers or gene mutation [85]. Since both cause a qualitatively similar range of DNA changes, somaclonal variation exhibits a similar spectrum of genetic variation to trigger mutation [86]. According to [87] oxidative stress damage done on plant sources during plant tissue culture may be the cause or a contributing factor in a large portion of the diversity observed in *in vitro* culture plants.

Increased quantities of pro-oxidants, or ROS, including hydrogen peroxide, superoxide, peroxyl, alkoxyl radicals, and hydroxyl, are a result of oxidative stress. Using the micropropagation

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technique, these ROS may result in mutations in plant cells (Fig. 2) , including altered hyper- and hypo-methylation of DNA [88], variations in chromosome number from polyploidy to aneuploidy, DNA base deletions and substitutions, chromosome rearrangements, and chromosome strand breakage [89]. The frequency of somaclone production under plant tissue culture settings was influenced by some factors, including the number of subculture cycles, the duration of the culture period , the manner of regeneration , the culture environment, and the explant source [85].

By exposing the tissue to salt stress and choosing cell cultures that exhibit resilience to salinity conditions, one can take advantage of the genetic variety produced by somaclonal variation [90]. Micropropagation of retrotransposons has also been demonstrated to promote somaclonal variation in *Oryza sativa* [91], and *in vitro*, culture-enhanced genotypic and phenotypic variants are combined and referred to as "somaclonal variation" [92]. Moreover, the physiological reactions of plant cells may be connected to epigenetic alterations, for example, DNA methylation and histone modifications [93].

Somatic crossover, point mutations, chromosome number changes, chromosome rearrangement and breakage, sister chromatid exchange, segregation of preexisting chimeric tissue, somatic gene rearrangement, DNA methylation, changes in organelle DNA, DNA amplification, RNA interference, histone modifications, epigenetic variation, and excision or insertion of transposable elements are some of the bases for somaclonal variation that have been proposed. More precisely, transposable elements are a major contributor to genomic rearrangements in plant tissue cultures [85].

Variations caused by tissue culture or pre-existing genetic variances in cells may cause somaclonal variation [94]. Different types of mutations, including de-amplification, gene amplification, duplication, deletion, inversion, reactivation of dormant genes, point mutations, or activation of transposable elements in multigene families, can produce the variation [95]. According to [96], tissue culture settings that include resistance to various stressors, pathogens, and illnesses have been shown to increase specific somaclonal variations. Although the exact mechanism of somaclonal variation is yet unknown, one of the primary reasons for somaclonal diversity in rice is the transposition of retrotransposons. [97].

Growth regulators had a beneficial effect on callus in terms of chromosomal instability and the high frequency of structural rearrangements in the cultured cells' chromosomes, with translocations/dicentrics and chromosome/chromatid swaps being the most common [98].

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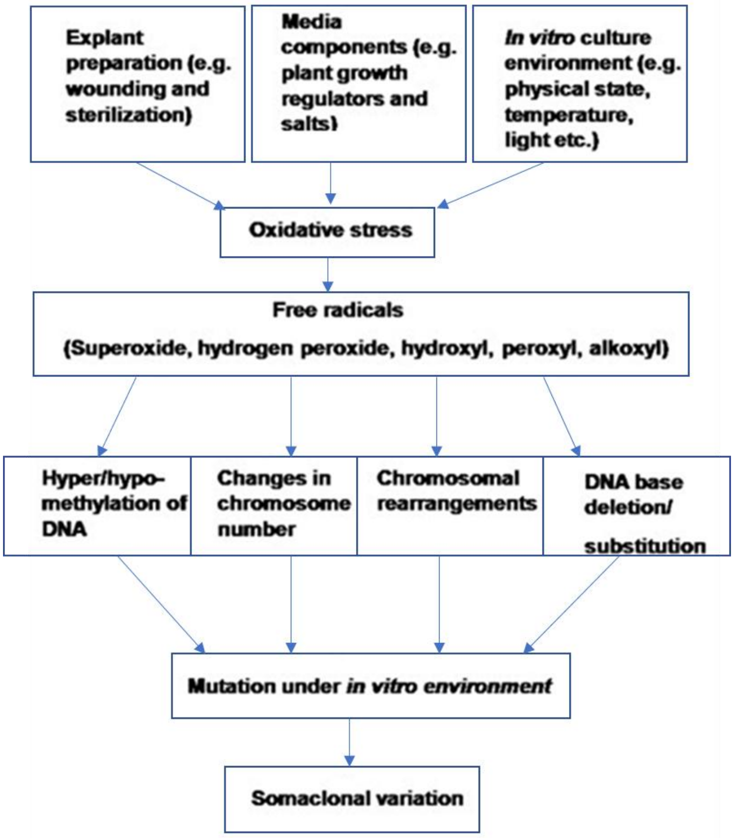

Fig. 2. The process by which oxidative burst during *in vitro* culture causes somaclonal variance in micropropagated plants. Source: Krishna et al. [85]

13.CONCLUSIONS

Plant transport mechanisms are impacted by salt stress, which may change the nutritional status and tissue ion balance. Mechanisms of salt adaptation that lead to improved long-term salinity tolerance may employ either the gene products from short-term salt stress or other means for increased resistance. Enhanced salt tolerance is likely achieved by the enhancement, activation, or maintenance of the function of physiological systems that are particularly sensitive to disruption by amplified concentrations of salinization. Plant cells have defense systems that can lessen the oxidative damage caused by ROS. The most popular method for detoxifying ROS produced by stress reactions is the enhancement of ROS-scavenging enzymes, for example, SOD, APX, CAT, and POD. Osmotic adjustment is generally linked to increased proline during salinity stress, which can improve plant cells' ability to withstand salt.

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Conflict of interests.

There are non-conflicts of interest.

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