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## Chapter

# The Biochemical Mechanisms of Salt Tolerance in Plants

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## Abstract

Salinity is one of the most severe environmental problems worldwide and affects plant growth, reproduction, and crop yields by inducing physiological and biochemical changes due to osmotic and ionic shifts in plant cells. One of the principal modifications caused by osmotic stress is the accumulation of reactive oxygen species (ROS), which cause membrane damage and alter proteins, DNA structures, and photosynthetic processes. In response, plants increase their arsenal of antioxidant compounds, such as ROS scavenging enzymes and nonenzymatic elements like ascorbate, glutathione, flavonoids, tocopherols, and carotenoids, and their rates of osmolyte synthesis to conserve ion homeostasis and manage salt stress. This chapter describes the principal biochemical mechanisms that are employed by plants to survive under salt-stress conditions, including the most recent research regarding plant tolerance, and suggests strategies to produce valuable crops that are able to deal with soil salinity.

**Keywords:** salinity, ROS, scavenging enzyme, antioxidant compound, osmolyte

## 1. Introduction

Salt stress in the form of soil salinity restricts plant growth and limits crop yields. Globally, soil salinity affects 6–10% of the total land surface (~ 800 million ha), 20–33% of which is used for agricultural purposes [1–3]. The damages caused by soil salinity are more notable in arid and semiarid regions where limited rainfall, high evapotranspiration rates, and extreme temperatures coupled with poor water and soil management practices exacerbate this problem [4, 5]. Despite the current agricultural problems due to soil salinity, world population growth has exerted substantial pressure for increased crop production to meet the global demand for food. Simultaneously, climate change has continued to markedly challenge the growth and production of agricultural crops due to variations in temperature, shifts in precipitation, reduced solar radiation, and increased evaporative demand.

Salinization can be the result of natural causes, such as flooding, wind erosion, and the redistribution of salts in shallow groundwater systems due to the weathering of minerals

and salty rocks that release sodium chloride (NaCl) and other soluble salts like magnesium, calcium, sulfates (SO<sub>4</sub>), and carbonates (CO<sub>3</sub>) into the environment [6, 7]. Other sources of salinity include high evaporation rates in the tropics and the precipitation of ocean salt by wind and rain, which increase ion concentrations in soils [8]. However, the global increase in salinization is mainly due to anthropogenic activities, such as irrigation, land clearing, deforestation, agricultural intensification, the use of imbalanced fertilizers, or poor drainage systems [7]. Irrigation practices have also elevated groundwater levels, resulting in a subsequent increase in evaporation. Moreover, industrial wastewater and effluents enriched in salts can elevate the salinity levels of agricultural soils.

Salinity has drastic consequences in plants at a physiological level because it restricts the ability of plants to take up water. In plants under salt-stress conditions, the rates of transpiration and photosynthesis decrease while the opening and closing of stomata is generally quick; in addition, ion toxicity, membrane instability, and mineral limitation are observed along with the inhibition of both enzymes and metabolic pathways [9–11]. Additional problems emerge when excessive amounts of salts enter a plant and reach toxic levels, impairing normal germination, plant growth, lateral bud development, productivity, and senescence [12]. The overall results of salinity stress can be seen in impaired plant growth, physiological functions, and crop yields, although these depend on the severity of the stress, the time scale of the response, and on whether the stress was abruptly or gradually imposed [11].

Plant damage caused by salinity primarily takes place in two phases. First, increases in soil salt content cause an osmotic effect, which reduces the soil water potential and consequently plant water absorption. Second, the excessive uptake of ions, mainly Na<sup>+</sup>, Cl<sup>-</sup>, and SO<sub>2</sub>, interferes with various metabolic processes in plants, including photosynthesis, nitrogen assimilation, malate metabolism, and protein translation [13]. This nutrient imbalance reduces the amounts of calcium, magnesium, and potassium in the plant [14]. In addition, oxidative damage is generated as a result of an increase in ROS due to a reduction in the rate of photosynthesis. The combination of these factors negatively affects plant functions, including those related to metabolism, and may damage plant structures, which can ultimately lead to plant death [15, 16].

The ability of crops to grow and reproduce in saline soil is dependent on the developmental stage of the plant and greatly differs between species, which is mainly due to the variability associated with limiting salt uptake from the soil and effectively compartmentalizing it at the cellular level [17]. To deal with the adverse effects of salinity, plants trigger different physiological and biochemical mechanisms that allow them to survive and grow, including salt exclusion, the control of ion uptake and translocation, ion compartmentalization within different cells and tissues, nutrient ion transport, the synthesis of compatible solutes and osmoprotectants, morphological and anatomical modifications, membrane and hormone changes, and antioxidative metabolism responses based on the production of antioxidant enzymes and compounds [8, 13, 18]. This chapter is focused on presenting the principal determinants of salt-stress tolerance in plants, which include the antioxidant defense system, enzymatic and nonenzymatic compounds, and the most important metabolites involved in osmotic adjustments.

## **2. Antioxidant defense mechanisms**

The antioxidant defense system is a vital mechanism by which plants deal with oxidative stress under saline conditions [19–21]. Salinization reduces the rate of

photosynthesis, which alters the electron flow from central transport chains to oxygen-reduction pathways, leading to an overproduction of ROS, such as superoxide radicals ( $O_2^{\bullet-}$ ), singlet oxygen ( $O_2$ ), hydrogen peroxide ( $H_2O_2$ ), hydroxyl radicals ( $OH^{\bullet}$ ), and alkoxy radicals ( $RO^{\bullet}$ ). ROS are generated in the cytosol, chloroplasts, mitochondria, and apoplastic spaces of cells [22–25]. Although ROS are formed in biological systems as by-products of respiration and photosynthesis, in low concentrations, they act as signal transduction molecules that are involved in mediating programmed cell death, development, and responses to pathogen infections and environmental stressors [23, 26]. However, an excess of ROS produces phytotoxic reactions, biomolecule oxidation, cell membrane damage, protein degradation, enzyme inhibition, and DNA mutations [27–29]. Therefore, fluctuations in the properties and functions of ROS will eventually lead to metabolic and physiological problems in plants.

The overproduction of ROS imbalances homeostasis at cellular and subcellular levels and may ultimately lead to cellular death [30]. The intensity of the oxidative stress depends on the types of ROS produced, their concentrations, the sites where they are released, interactions with other cellular molecules, and the developmental stage and potential of the cell [31]. To avoid damage caused by the overproduction of ROS, plants employ an antioxidant defense mechanism that contains several enzymatic and nonenzymatic constituents that mitigate potential negative effects by converting ROS into less toxic molecules [32]. Given that increases in antioxidant levels usually improve plant tolerance, an adjustable control system that balances ROS production and scavenging via antioxidant enzyme and nonenzyme activities is essential for limiting toxicity levels in plants under adverse conditions [33, 34].

Plants rely on enzymes that are specifically involved in ROS detoxification, namely those that act to lower ROS levels or avoid oxidative stress, including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and other enzymes involved in the AsA-GSH cycle, such as glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR). These antioxidant enzymes are located in different sites within plant cells and work together to detoxify ROS [35]. In addition, low molecular mass antioxidant compounds like ascorbate, glutathione, flavonoids, tocopherols, and carotenoids are also crucial for ROS homeostasis in plants [36–38].

## **2.1 Enzymatic antioxidants**

### *2.1.1 Superoxide dismutase*

Superoxide dismutase, which shows great variation across different plant species, is a metalloenzyme that plays an important role in combating oxidative stress in all subcellular organelles sensitive to ROS (i.e., chloroplasts, mitochondria, peroxisomes). This metalloenzyme catalyzes the dismutation of  $O_2^{\bullet-}$  into  $O_2$  and  $H_2O_2$ . A particularly interesting property of SODs is that they can only react with  $O_2^{\bullet-}$  through diffusion and electrostatic guidance at limited rates, yet they are highly effective at removing  $O_2^{\bullet-}$  [39]. SOD enzymes can be classified into three types according to their metal cofactors: copper/zinc (Cu/Zn-SOD; found in the cytosol or in plastids), manganese (Mn-SOD; found in mitochondria and peroxisomes), or iron (Fe-SOD; found in chloroplasts). Of note, it is only plants that have all three SOD types [39]. Superoxide dismutases are considered the first line of defense against ROS because an increase in SOD activity has been frequently

linked to improved plant tolerance in the presence of environmental stress [40]. For example, the overproduction of SOD has been found to enhance salt-stress tolerance in sweet potatoes [40]. Moreover, SOD activity has been put forth as an indirect means to screen for plants that are salinity resistant.

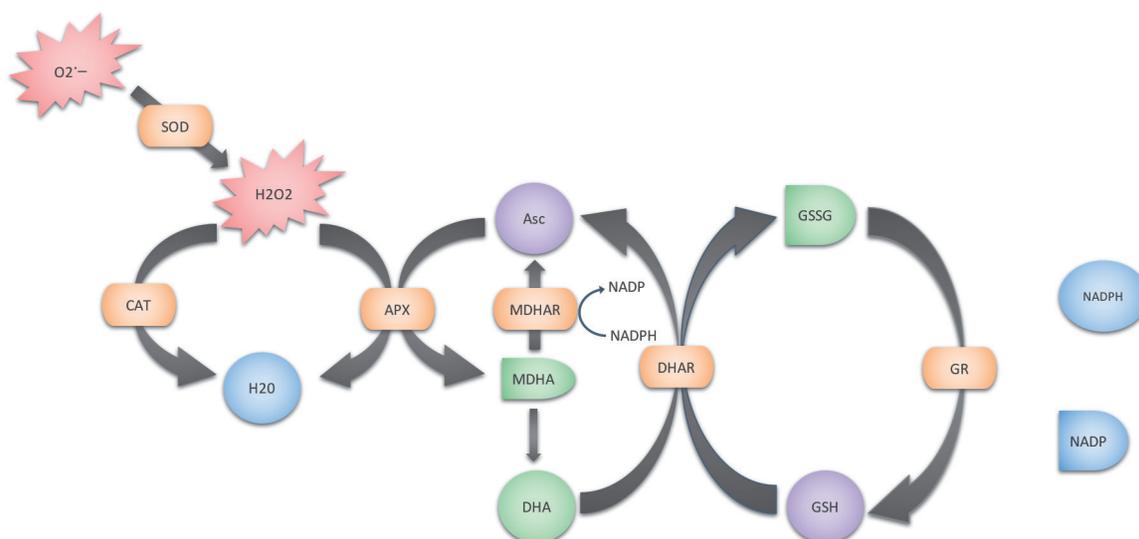
### *2.1.2 Catalase*

Catalase was the first enzyme to be identified with antioxidant capabilities and is mainly found in peroxisomes and glyoxysomes. The function of CAT is to convert H<sub>2</sub>O<sub>2</sub> into H<sub>2</sub>O and O<sub>2</sub> [41]. H<sub>2</sub>O<sub>2</sub> has been found to be produced in cell organelles during photorespiratory oxidation, the  $\beta$ -oxidation of fatty acids, purine catabolism, and because of the activities of enzymes, such as xanthine oxidase and SOD [42]. CAT plays a dynamic role in eliminating H<sub>2</sub>O<sub>2</sub> by degrading it in an energetically efficient manner. For example, one CAT molecule can transform about 6 million H<sub>2</sub>O<sub>2</sub> molecules into H<sub>2</sub>O and O<sub>2</sub> in roughly one minute [43, 44].

Whereas animals contain a single CAT gene, plants have a multigene family that includes multiple isoenzymes (depending on the species) whose expression is regulated according to how they are distributed within tissues or organs and the environmental conditions present [44]. In plants, there are three classes of catalases that are determined based on location: class I (photosynthetic tissues), class II (vascular tissues), and class III (seeds and young seedlings) [45]. A concomitant increase in CAT activity has been observed as part of the antioxidant defense system in plants. This increase may be a manifestation of the adaptive responses of plants to abiotic stress. It may also be assumed that without any concomitant increase in CAT activity, plant growth is likely to be severely limited. Therefore, different environmental stressors constitute major drivers that either enhance or restrict CAT activity, depending on the intensity, duration, and type of stress [46].

### *2.1.3 Enzymes involved in the AsA-GSH cycle*

The Asa-GSH cycle, also known as the Halliwell–Asada cycle, is a series of coupled redox reactions involving four enzymes: APX, MDHAR, DHAR, and GR [47]. This cycle plays a crucial role in the antioxidant protection system in the presence of H<sub>2</sub>O<sub>2</sub>, which is generated in different cellular compartments like chloroplasts, mitochondria, peroxisomes, and the cytosol and apoplast [48, 49]. H<sub>2</sub>O<sub>2</sub> is scavenged by APX via the oxidation of ascorbate. This enzyme comprises a family of five APX isoforms that are located in several organelles and cellular compartments, including glyoxysomes (gmAPX), thylakoids (tAPX), the cytosol (cAPX), mitochondria (mAPX), and soluble chloroplast stroma (sAPX) [46]. APX uses two molecules of ascorbate to reduce H<sub>2</sub>O<sub>2</sub> to H<sub>2</sub>O and produces two molecules of monodehydroascorbate (MDHA) from the oxidation of ascorbate. MDHA is converted back to ascorbate by MDHAR, which is a flavin adenine dinucleotide (FAD) enzyme with high specificity for MDHA. Subsequently, MDHA is further rapidly converted to dehydroascorbate (DHA) by the monomeric thiol enzyme DHAR. DHAR uses reduced glutathione (GSH) as the reducing substrate, which is regenerated by GR from its oxidized form glutathione disulfide (GSSG), and NADPH molecules act as donors of reducing equivalents [29, 43]. Recent studies have shown that these enzymes become active and participate in the ascorbic acid-glutathione cycle under salt-stress conditions, indicating that their increased activity may improve plant tolerance [50–52]. **Figure 1** shows the functions of the antioxidant enzymes described above.



**Figure 1.**  
The orange squares show ROS scavenging by the antioxidant enzymes superoxide dismutase (SOD) and catalase (CAT) and the enzymes involved in the Asa-GSH cycle, namely ascorbate peroxidase (APX), monodehydroascorbate (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). The purple circles show the nonenzymatic antioxidant compounds glutathione and ascorbate that are described in section 2.2. The diagram was modified from [48].

## 2.2 Nonenzymatic antioxidants

### 2.2.1 Ascorbic acid

Ascorbic acid (well known as Vitamin C) is the main antioxidant in plants and acts as a major redox buffer and cofactor for enzymes. The structure of ascorbic acid is like those of hexose sugars and is comprised of a conjugated structure composed of a five-carbon lactone ring, containing enediol groups on C2 and C3. Ascorbic acid is considered to be the most powerful ROS scavenger due to its ability to donate electrons to a wide range of electron receptors in several enzymatic and nonenzymatic reactions [53]. Ascorbic acid protects cellular membranes by directly scavenging  $O_2\bullet-$  and OH while acting as a cofactor for violaxanthin deepoxidase, sustaining the dissipation of excess excitation energy in chloroplasts [54]. In addition, ascorbic acid has the redox potential to interact with hydroxyl radicals, superoxides, oxidized glutathione, and tocopherol radicals [53, 55].

Ascorbic acid is involved in many plant pathways related to photosynthesis, hormone biosynthesis, antioxidant regeneration, defense responses, signal transduction, flowering, cell division, and growth and is abundantly found in meristems and photosynthetic cells [56, 57]. Under normal physiological conditions, ascorbic acid largely remains in a reduced form in leaves and chloroplasts [55] and accumulates in photosynthetic organs, although it can be found in high concentrations in non-photosynthetic tissues with the amounts varying depending on the plant species, variety, tissue type, and growth environment [53, 58].

Multiple experiments have been developed to evaluate the roles of antioxidant compounds, such as glutathione and ascorbic acid, when they are applied to different plant tissues. For example, Aliniaiefard et al. [59] sprayed 2 mM AsA and 3 mM GSH on olive plants treated with 100 mM NaCl and reported that plant growth parameters significantly improved with the application of AsA when compared with those of the plants sprayed with GSH. In addition, the Na<sup>+</sup> and Cl<sup>-</sup> concentrations decreased in the olive plants sprayed with AsA while the K<sup>+</sup> concentration and K/Na ratio increased.

Aliniaiefard et al. concluded that the exogenous application of AsA is recommended for improving the tolerance of olive plants under saline conditions. Similarly, Sadak [60] applied AsA to flax cultivars irrigated with salt water and found that AsA allowed for an increase in antioxidant defense via the activation of ROS scavenging enzymes.

### 2.2.2 Glutathione

Together with ascorbic acid, glutathione is one of the most important nonenzymatic antioxidants. Glutathione is a thiol tripeptide composed of  $\gamma$ -glutamyl-cysteinylglycine and plays a central role in antioxidant defense by scavenging ROS, thereby maintaining redox homeostasis in plant tissues [61]. The chemical reactivity, relative stability, and high water solubility of the thiol group of glutathione makes it ideal for protecting plants against oxidative stress or stress due to heavy metals and exogenous or endogenous organic chemicals [62]. Glutathione is localized in all cell compartments, such as the chloroplasts, cytosol, vacuoles, mitochondria, and endoplasmic reticulum. In physiological processes, glutathione plays important roles in xenobiotic detoxification, metabolite conjugation, signal transduction, and stress-responsive gene expression [61, 63]. Glutathione also participates in tissue growth and development, cell death and senescence, and the enzymatic regulation of pathogen resistance [64].

Glutathione also appears to be important in controlling  $O_2^{\bullet-}$ ,  $\bullet OH$ , and  $H_2O_2$  levels in cells under stressful conditions given the observed changes in the ratio of its reduced (GSH) and oxidized (GSSG) forms, which provides information on the cellular redox balance [65, 66]. GSH is required for GRX-mediated dithiol and monothiol reduction mechanisms and is important for the activation of GPX, GST, and glyoxalase functions, particularly recycling GSH from GSSG in the presence of NADPH. Therefore, GSH plays a key role in ROS tolerance under oxidative stress in association with other ROS-metabolizing enzymes [57]. In addition, the primary reaction in plants when they are exposed to progressive salinity is the oxidation of GSH, indicating that this reaction is an early response to oxidative stress [33, 67].

Studies have demonstrated the benefits associated with the application of GSH in modulating salt-stress tolerance and positively influencing yield-contributing traits in plants like rice (*Oryza sativa* L.) [68], while the application of GSH has been found to increase the transcript levels and activities of genes and enzymes related to GSH synthesis and metabolism in tomato plants (*Solanum lycopersicum*) [69].

### 2.2.3 Flavonoids

Flavonoids are largely responsible for the pigmentation of seeds, flowers, stems, roots, and fruits. Flavonoids are aromatic compounds that are derived from chalcone, which is obtained from phenylalanine and malonyl-coenzyme A. According to their chemical structures, flavonoids can be classified into flavones, flavanones, flavonols, flavans, flavandiols, isoflavones, anthocyanins, and condensed tannins [70, 71].

Flavonoids act to prevent ROS increase through the inhibition of ROS-generating enzymes, including cyclooxygenase, lipoxygenase, monooxygenase, and xanthine oxidase. The ability to chelate metals is essential for impeding the regeneration of radical ROS molecules, such as superoxide, hydroxyl radicals, and hydrogen peroxide [72, 73]. Given that they contain functional hydroxyl groups, flavonoids constitute a secondary antioxidant system, as they support the function of other ROS scavenging systems when the activities of antioxidant enzymes are reduced. In addition, flavonoids serve as antioxidant barriers that protect cellular components against oxidizing pollutants

like ozone (O<sub>3</sub>) and sulfur dioxide (SO<sub>2</sub>). Due to their elevated abilities to donate electrons or hydrogen atoms, the antioxidant capacities of flavonoids have been found to be many times higher than those of either ascorbic acid or α-tocopherol [74, 75].

Interestingly, in *Ginkgo biloba* seedlings, treatment with 100 mmol/L NaCl was found to improve the biosynthesis of flavonoids and flavonol [76]. In addition, the upregulated expression of five flavonoid biosynthesis-related genes was also detected. The authors indicated that *G. biloba* seedlings could tolerate low-level soil salinity stress via the regulation of flavonoid biosynthesis, which was accelerated in response to environmental stress.

#### 2.2.4 Tocopherols

Tocopherols constitute a group of lipophilic compounds that are important antioxidant and nonenzymatic components capable of inhibiting lipid peroxidation. Tocopherols are also essential for maintaining membrane integrity. These lipophilic compounds are synthesized from homogentisic acid and isopentenyl diphosphate in the plastid envelope. Tocopherol exists in four isomeric forms (α-, β-, γ-, and δ-), with the predominant forms being α- and γ-tocopherol. The composition of tocopherol depends on the genotypic features of the plant, growth conditions, tissue type, and stress intensity. Tocopherols are present in seeds, fruits, roots, tubers, cotyledons, hypocotyls, stems, leaves, and flowers. In addition, α-tocopherol may regulate the concentrations of plant hormones, such as jasmonic acid, which control both growth and development [38, 77].

As a component of thylakoid membranes, tocopherol acts as an important scavenger of O<sub>2</sub> and OH while maintaining a stable redox status and the structure and function of PSII. Tocopherols have also been found to reduce lipid peroxyl radicals (obtained from lipid peroxidation) to their corresponding hydroperoxides [78]. In addition, tocopherols participate in cell signaling and they may protect embryos during germination from ROS, senescence, and stress [79, 80]. Recent studies have also shown that tocopherol plays a positive role under salt-stress conditions by controlling Na<sup>+</sup>/K<sup>+</sup> homeostasis and the hormonal balance while minimizing oxidative stress [81]. Additionally, it has been demonstrated that the foliar application of α-tocopherol in onion plants and *Vicia faba* improve salt tolerance with an increase in plant growth and productivity in this condition [82, 83].

#### 2.2.5 Carotenoids

Carotenoids are hydrophobic pigments derived from isoprene that play essential roles in photosynthesis and nutrition and protect against photo-oxidative damage in higher plants [37]. Carotenoids are mainly present in the form of 40-carbon tetraterpene, which consists of eight isoprene units [84]. In plants, carotenoids are synthesized in plastids from isoprenoid precursors. Lycopene is a principal carotenoid and is a product of the sequential desaturations of phytoene and may be converted into β-carotene by lycopene β-cyclase (Lcy-b) [85, 86]. Carotenoids act as light harvesters by dissipating excess energy as heat, and they also protect the photosynthetic apparatus from the free radicals produced during photosynthesis by stabilizing photosystem I and II and the thylakoid membrane. Furthermore, carotenoids are precursors of hormones like abscisic acid and strigolactones [87].

Carotenoids quench the O<sub>2</sub> and H<sub>2</sub>O<sub>2</sub> formed under salt stress due to their low triplet state energy and in this way, protect lipids from peroxidation while suppressing

radical chain reactions [88–90]. Li et al. [91] recently showed that the overexpression of three genes associated with carotenoid biosynthesis from *Lycium chinenses* enhanced salt tolerance in tobacco plants and suggested that plants may synthesize and accumulate more carotenoids under salt-stress conditions, showing higher resistance to oxidative stress, by an increase of the expression level and activity of antioxidant enzymes.

### 3. Osmolytes that maintain cell turgor

Salinity decreases the osmotic potential of soil, which in turn limits water absorption by plants. In addition, the toxicity of Na<sup>+</sup> and Cl<sup>-</sup> impedes the uptake of essential nutrients. In particular, Na<sup>+</sup> toxicity can disrupt the absorption of K<sup>+</sup> and Ca<sup>2+</sup>, favoring the production of ROS and inducing oxidative damage [92].

Plants have developed responses to deal with water loss and the transport and accumulation of toxic ions. Given that water loss in plants originates due to the low

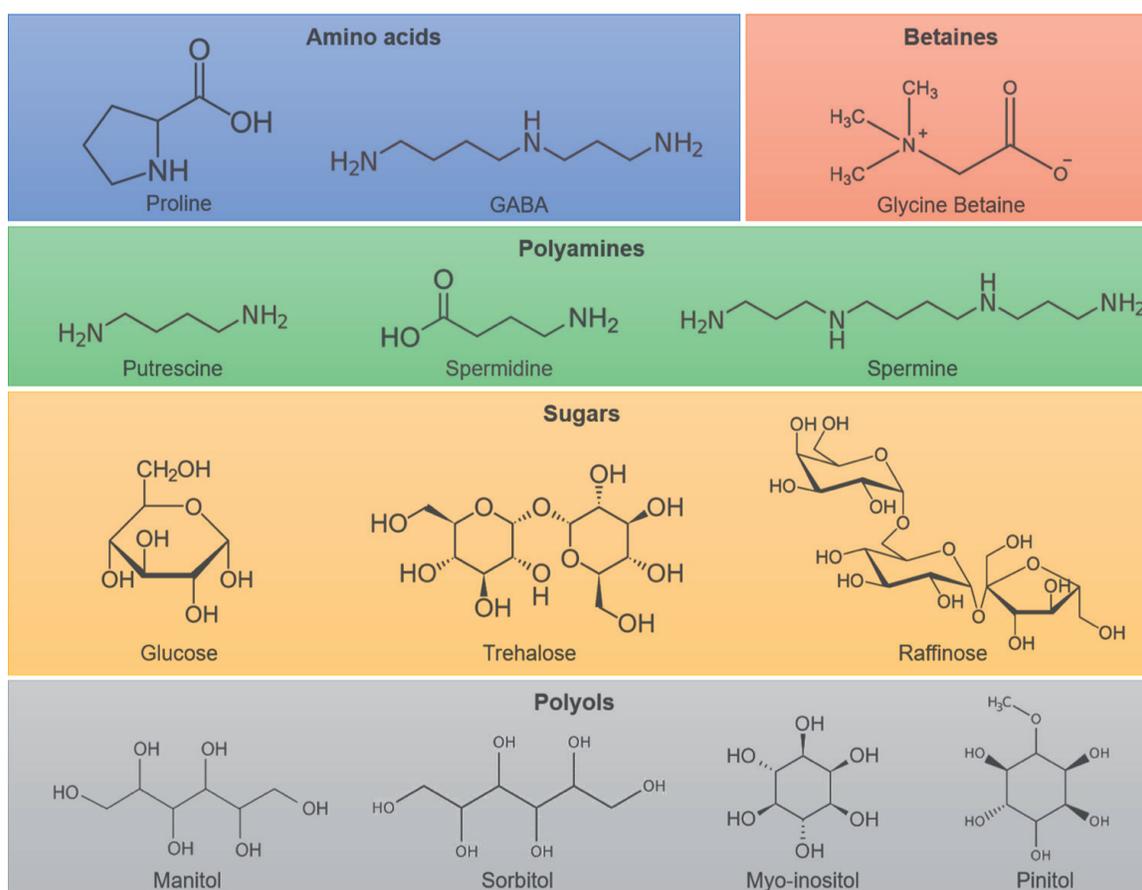
	Type of study	Species	Reference
<b>Amino acids</b>			
Proline	Exogenous application	<i>Solanum lycopersicum</i> , <i>Glycine max</i> , <i>Pisum sativum</i>	[102–104]
GABA	Natural accumulation	<i>Nicotiana tabacum</i> and <i>Sorghum bicolor</i>	[105, 106]
<b>Polyamines</b>			
Putrescine	Natural accumulation	<i>Cajanus cajan</i>	[107]
Spermidine	Exogenous application	<i>Oryza sativa</i>	[108]
Spermine	Natural accumulation	<i>O. sativa</i>	[109]
<b>Betaines</b>			
Glycine betaine	Exogenous application	<i>O. sativa</i> , <i>Glycine max</i> , and <i>Phaseolus vulgaris</i>	[110–112]
<b>Sugars</b>			
Glucose and fructose	Natural accumulation	<i>Vitis vinifera</i> and <i>Lepidium crassifolium</i>	[113, 114]
Trehalose	Transgenic expression	<i>O. sativa</i>	[115]
Raffinose	Transgenic expression	<i>Arabidopsis thaliana</i>	[116]
<b>Polyols</b>			
Mannitol	Transgenic expression	<i>N. tabacum</i>	[117]
Myo-inositol and pinitol	Transgenic expression	<i>N. tabacum</i>	[118, 119]
GABA = Gamma amino butyric acid			

**Table 1.** Studies in plants that directly correlate metabolite accumulation to increased salinity stress tolerance.

osmotic potential of the soil, plants must employ compensatory mechanisms [93]. Plant cells permit higher influxes of Na<sup>+</sup>, which decrease the water potential and cause osmotic stress in cells. Salts are translocated from the roots to shoots to maintain ion homeostasis, although this reduces photosynthetic efficiency due to the inhibition of photosystem II (PSII) [94]. To cope with osmotic stress and maintain ion homeostasis, plants biosynthesize osmolytes.

Osmolytes or compatible solutes are small molecules with low molecular weights that are electrically neutral, highly soluble, and do not affect normal biochemical processes [95]. The biosynthesis and accumulation of osmolytes constitutes an essential protection strategy for plants under abiotic stress. Multiple studies have elucidated the roles that osmolytes play in abiotic stress tolerance due to natural accumulation [96, 97], exogenous application [98, 99], or the transgenic expression of osmolyte pathway genes [100, 101], which are summarized in **Table 1**.

The primary function of osmolytes is to accumulate inside the cell to maintain the osmotic balance between the plant cell and its surroundings [120]. Osmolytes can also act as chemical chaperones by stabilizing and protecting proteins and membranes [121] or by acting as ROS scavengers [122]. Some of these compatible solutes are highly effective in reducing the extent of K<sup>+</sup> loss in response to salt stress [123]. Overall, osmolytes are chemically diverse, although they can be broadly grouped into amino acids, polyamines, betaines, sugars, and polyols, which are shown in **Figure 2**.



**Figure 2.** Chemical structures of the most common osmolytes observed in salt-stress responses in plants. These structures can be grouped into amino acids, polyamines, betaines, sugars, and polyols.

### 3.1 Amino acids

Amino acids are the building blocks of proteins, which carry out many biological processes and provide structure and support for cells [124]. In addition, many studies have reported the accumulation of amino acids in plants exposed to drought and salinity conditions [97, 98, 125, 126]. This accumulation may be due to elevated amino acid production and/or the stress-induced breakdown of proteins [127]. Some of the amino acids that have been found to accumulate are alanine, arginine, glycine, serine, leucine, valine, and proline, in addition to non-protein amino acids like citrulline, ornithine, and gamma amino butyric acid (GABA) [128, 129].

Proline is the most important osmolyte and signaling molecule and generally accumulates in the cytosol. Proline also acts as an ROS scavenger and molecular chaperone, stabilizing the structure of proteins and protecting cells from potential damage induced by osmotic and oxidative stress [120, 130, 131]. Proline is mainly synthesized from glutamate by  $\Delta$ 1-pyrroline-5-carboxylate (P5C) synthetase and P5C reductase enzymes, although under nitrogen-limited conditions, proline is synthesized in the ornithine pathway and transformed into P5C/GSA (glutamate-1-semialdehyde) via ornithine- $\delta$ -aminotransferase [132, 133].

Proline has been associated with increased salt tolerance in tomato (*Solanum lycopersicum*) [102], soybean (*Glycine max*) [103], groundnut (*Arachis hypogaea*) [134], pea (*Pisum sativum*) [104], sainfoin (*Onobrychis viciaefolia*), and mung bean (*Vigna radiata*) plants [100]. Researchers have also reported that the exogenous application of proline enhances its endogenous level, thus promoting growth and the antioxidant defense system and decreasing the uptake rate of Na<sup>+</sup> and Cl<sup>-</sup> [99, 135].

Gamma amino butyric acid is a four-carbon non-protein amino acid with an amino group attached to  $\gamma$ -carbon instead of  $\alpha$ -carbon. GABA is mainly synthesized from glutamate in the cytosol by glutamate decarboxylase and then transported to the mitochondria [136]. GABA metabolism has been associated with the carbon/nitrogen balance and ROS scavenging [137, 138]. In addition, GABA accumulation and metabolism have been found to be activated by salt exposure in tobacco plants [105]. Moreover, GABA-T *Arabidopsis* mutants have been found to be hypersensitive to ionic stress, showing elevated levels of amino acids (including GABA) [139]. In sorghum, GABA may also contribute to CSF20 osmoregulation and signaling to increase salt tolerance [106].

### 3.2 Polyamines

Polyamines (PAs) are low molecular weight aliphatic nitrogenous bases containing two or more amino groups [140]. The most common PAs in higher plants are putrescine, spermidine, and spermine. Putrescine can be produced from ornithine by ornithine decarboxylase or from arginine by arginine decarboxylase. Putrescine is then converted to spermidine (spermidine synthase) and spermidine into spermine (spermine synthase). Both spermidine and spermine can be converted back to putrescine by polyamine-oxidases [36].

PAs regulate diverse cellular functions that are essential for cell growth, including senescence, development, cell proliferation, and signal transduction while also regulating the expression of genes in response to various stressors. However, PA accumulation has been detected in plants under abiotic stress [141]. Polyamines act as osmolytes due to their ability to block ion channels (cationic structures) and scavenge ROS [36]. Exogenous spermidine treatment in both salt-sensitive and salt-tolerant rice cultivars has been found to result in plasma membrane recovery after injury induced by salinity

[108]. In addition, the exogenous application of spermidine and putrescine was found to increase the postharvest shelf-life of *Capsicum annuum* [142], while improving grain filling and drought tolerance in wheat plants [143]. It has also been reported that putrescine exhibits salinity tolerance in the pigeon pea (*Cajanus cajan*) by modulating the anabolic and catabolic enzyme activities responsible for putrescine biosynthesis [107].

### 3.3 Betaines

Glycine betaine (GB) is a quaternary ammonium compound whose distribution among plants is restricted to certain species like *Arabidopsis*, and many crop plants do not accumulate it [144]. This organic compound is mainly localized in chloroplasts and plays a vital role in chloroplast adjustments and the protection of thylakoid membranes, which helps to maintain the photosynthetic efficiency of the plant [145, 146]. At the same time, GB encourages water to flow into cells, which helps to maintain intracellular osmotic equilibrium and regulates the signaling transduction cascade under stressful conditions [147]. GB is synthesized in chloroplasts from serine via ethanolamine, choline, and betaine aldehyde. Choline is converted to betaine aldehyde by choline mono-oxygenase, which is then converted to GB by betaine aldehyde dehydrogenase [148].

The exogenous application of GB mitigates the adverse effects of salinity stress in some plant species. For example, the foliar application of GB was found to result in significantly improved salt tolerance in rice plants [110], and the exogenous application of GB on tomato plants subjected to salt stress resulted in an increase in fruit yield of ~40% compared with that of untreated plants [149]. Salinity tolerance in response to GB has also been observed in mung bean (*V. radiata*) [150], green bean (*Phaseolus vulgaris*) [108], and soybean (*G. max*) plants [111].

### 3.4 Sugars

Sugars provide carbon and energy for cellular metabolic processes while regulating plant growth and development. However, under stressful conditions, carbohydrate metabolism results in an increase in sugar levels. The production and collection of soluble sugars directly contributes to ROS scavenging, osmotic adjustments, carbon storage, and the stabilization of protein structures like Ribulose-1,5-bisphosphate carboxylase–oxygenase [151]. Sugars are also the main osmolytes that participate in osmotic adjustments and can contribute up to 50% of the total osmotic potential in some plant species [152]. Structurally, all kinds of sugars have been reported in response to salinity, including monosaccharides (glucose and fructose), disaccharides (trehalose and sucrose), and oligosaccharides (raffinose family) (**Table 1**).

Studies have shown that plants mobilize starch and fructans from storage organs (roots, stems, and amyloplasts in leaves) to increase the accumulation of sugars, such as glucose, fructose, and sucrose. Starch hydrolysis by the  $\alpha$ -amylolytic pathway represents the primary means of starch degradation in leaves under normal growth conditions and may also be involved in stress-induced starch hydrolysis. Downton [113] shows that *Vitis vinifera* salt-stressed leaves contained decreased amounts of sucrose and starch but increased levels of reducing sugars. Rathert [153] showed that salt stress induced the restricted utilization of leaf sucrose but not of foliar starch in *G. max* varieties. In addition, Murakeözy et al. [114] found a high accumulation of soluble carbohydrates in *Lepidium crassifolium* (Brassicaceae) leaves in response to salinity.

Similarly, trehalose accumulates in many organisms due to various abiotic stressors and has been reported to act as an osmolyte [154]. Trehalose is a disaccharide that is

synthesized by a two-step process in which trehalose-6-phosphate is first synthesized from glucose-6-phosphate and then dephosphorylated to trehalose by trehalose-6-phosphate phosphatase [155]. Several studies have evaluated the transgenic expression of trehalose biosynthesis genes, which have been shown to enhance trehalose metabolism and tolerance to abiotic stress. For instance, the overexpression of *otsA* and *otsB* in transgenic rice plants was found to result in the increased accumulation of trehalose content and an overall improved photosynthetic capacity, reducing oxidative damage and improving ion uptake and partitioning under conditions of salt stress [115]. Also, the induction of *OsTPP1* and *OsTPP2* by the exogenous application of ABA was found to enhance cold, salinity, and drought tolerance in rice plants [156].

The raffinose family oligosaccharides (RFO), such as raffinose, stachyose, and verbascose, are macromolecules that act to protect plants from drought, salt, cold, freezing, and oxidative stress [157]. In addition, RFOs have been implicated in membrane protection and radical scavenging. Furthermore, *Arabidopsis* plants overexpressing *Arabidopsis* *GolS1* or *GolS2* were found to accumulate high levels of galactinol and raffinose and were more tolerant to salinity stress [116].

### **3.5 Polyols**

Polyols or sugar alcohols are polyhydric alcohols that are widely distributed in the plant kingdom, and they can be grouped into linear and cyclic structures. The most common polyols are mannitol, glycerol, sorbitol (linear), and myo-inositol, along with the methylated derivatives ononitol and pinitol (cyclic) [158, 159]. Polyols accumulate in the cytoplasm and act as osmoprotectants and ROS scavengers, preventing water loss and oxidative damage to membranes and enzymes. Polyols originate via the reduction of aldoses or their phosphate esters and are generally water soluble in nature [160].

Williamson [161] reported that mannitol, sorbitol, and inositol increase drought and salinity tolerance in some plants. Transgenic tobacco plants overexpressing bacterial mannitol-1-phosphate dehydrogenase were found to accumulate high concentrations of mannitol in their leaves and roots and exhibited a high degree of salt tolerance [101]. Moreover, Adams et al. [162] reported that myo-inositol, ononitol, and pinitol accumulated under salt-stress conditions in several halotolerant plant species. Furthermore, the over-expression of *MIPS* and *IMT* from halotolerant plants was found to increase cyclic polyol levels and salt-stress tolerance in tobacco plants [118, 119].

## **4. Conclusions and perspectives**

Salt stress is one of the most important factors that limits the productivity of agricultural crops and threatens global food security. Salinity produces osmotic stress and ionic toxicity in plants, which alters cell homeostasis and reduces plant water absorption, adversely affecting growth and plant productivity. Osmotic imbalances have been found to cause an overproduction of ROS that leads to the oxidation of biomolecules, cell membrane damage, protein degradation, enzyme inhibition, DNA mutations, and cellular death. To limit the damage, cells turn on enzymatic and nonenzymatic antioxidant machinery. The ROS detoxification system is very complex and controlled at multiple levels because ROS participate in biological processes like photosynthesis, signal transduction, development, and programmed cell death. Therefore, to evaluate the negative and positive roles of ROS, it is important to understand tolerance mechanisms in plants and the ability to control or moderate

ROS levels. Recently, it has been proposed that ROS homeostasis may be modulated through the use of nanoparticles that activate the expression of antioxidant enzyme genes or that have the ability to scavenge ROS [22], thus improving salt tolerance.

Another response to salinity in plants is the induction of osmolyte biosynthesis to stave off water loss and the accumulation of toxic ions. The production and accumulation of osmolytes inside the cell is essential for the protection and survival of plants under salt stress and other forms of environmental stress, although their production is taxonomically restricted. It has been shown that the exogenous application of osmolytes, such as aminoacids, betaines, or sugars, and the overexpression of osmolyte genes constitute viable options to improve plant resistance to salinity. Thus, the use and application of osmolytes in agricultural settings should continue to expand. Current studies have shown that when taken together, metabolic and physiological plant responses can provide valuable information of the possible mechanisms required for plants to adapt to stress. Thus, modulating one component of the antioxidative defense system or a particular metabolite might be insufficient to confer resistance to the entire plant. To generate salt-tolerant species, it is essential to use modified plants that incorporate more than one component, such as the use of multiple antioxidants or metabolites or a combination of both. In this way, further progress in genomics, proteomics, and metabolomics, together with improvements in biotechnological tools, will allow for the underlying mechanisms of salt-tolerant species to be fully elucidated and understood.

## Acknowledgements

We would like to thank Programa para el Desarrollo Profesional Docente (PRODEP), University of Guadalajara, Consejo Nacional de Ciencia y Tecnología (CONACYT), and Laboratorio Nacional PlanTECC for the use of facilities and the support provided via the project 315918.

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