Review paper

Salt stress and tolerance mechanisms by plants

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Abstract

Salinity stress has remained a hot threatening topic towards population explosion due to the shrinkage of agricultural land. A natural process, soil salinity is further worsening by anthropogenic activities. The result is decline in plant growth performance and crop productivity. In the present review we have discussed the negative impact of NaCl stress on plants by enhancing ROS formation since sodium chloride represents a wide spread salt, responsible for plant stress. Further, their quenching by various physiological and biochemical activities triggered by plants are also presented in the review. Increasing antioxidants, compatible solutes, and ion homeostasis help in tolerant as well as sensitive plants to overcome stress. But among different species, the range of tolerance persists over a specific time and depends upon genotype of the species. Furthermore, besides antioxidants and osmolytes, the role of various organelles during stress is also discussed. In conclusion, understanding their mechanism at various levels may help to get plants with a range of tolerance at different growth stages, when subjected to salt stress. So, increasing crop productivity might replenish the need for food over population burst in future.

Keywords: antioxidants, organelle stress, osmolytes, ROS, salt stress

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Introduction

Global climate changes led by natural and anthropogenic activities are increasingly challenging crop husbandries. Of these challenges, abiotic stresses are particularly considered as the major threat to global agricultural production (Khan et al., 2015). Because of their sessile nature, plants are continuously facing harsh environmental conditions. Amongst abiotic stressors, salt, drought, heat, chilling, and heavy metals are common and widespread (Wani et al., 2013). NaCl, as an abiotic stressor, hampers plant's development and growth, limiting crop production worldwide (Mbarki et al., 2018). It is attributed to the billion dollars of loss annually and is becoming worse due to accelerated anthropogenic activities and other climatic changes (El-Ramady et al., 2019; Farooq et al., 2020). High salinity has affected both cultivated (20%) (Ke et al., 2018) and irrigated land (1/3) worldwide (Food, 2011). In South-Asia and India around 52 million hectares and 6.73 million hectares of land are hampered, respectively by salinity (Sharma and Singh, 2015). The loss of crop output has an estimated annual global cost of 27.3 billion US dollars (Cherlet et al., 2018).

It is estimated that over 50% of the cultivated land is going to be lost as a result of salinity by 2050 (Shrivastava and Kumar, 2015). To achieve the target of feeding population, crop productivity

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must be increased to 70% by 2050 (Munns and Tester, 2008). However, it seems a harder challenge to target the ratio of feeding people due to shrinkage of agricultural land (primarily due to industrialization), poor soil drainage system, and natural factors. In scientific terms, the big problem is limited knowledge about and understanding of the fundamental mechanisms related to sensing and signaling in salinized plants. Therefore, the main aim of salinity research is to understand how tolerant plants cope with salinity when grown in saline environment. So, tolerant species can be developed based on new gene techniques, without spending huge amount for saline soil reclamation.

Soil is considered as saline when its electrical conductivity is 4 dS·m^{-1} or equal to 40 mM NaCl (Munns and Tester, 2008). In other words, soil salinity is defined as the presence of excess salts surrounding the rhizosphere, thereby restricting upward movement of essential elements and water from the soil. Salinity stress defined in terms of osmotic stress, ion toxicities, and oxidative stress exerts threefold effect on plants by reduced growth, yield, and quality of yield (Khare et al., 2015). Various types of salt ions may accumulate in soil, e.g. $\mathrm{K^+}$, $\mathrm{SO_4^{2-}}$, $\mathrm{Ca^{2+}}$, NaCl, $\mathrm{Mg^{2+}}$, and $\mathrm{NO^{3-}}$, among which salts sodium chloride accumulation is wide spread and the most soluble salt resulting in plant stress (Talon et al., 2020). All plants have regulated sodium chloride accumulation mechanisms at low concentrations (Munns and Tester, 2008). In practice, if salt concentration is very high, it leads to plant demise.

The immediate and preliminary constraint of NaCl stress is osmotic stress, which restricts extraction of water and nutrients by roots. As a consequence, it causes stomatal closure, inhibition of cell expansion, and division of both roots and shoots, and therefore, reduction in growth is commonly observed phenomenon (El-Ramady et al., 2018; Munns and Tester, 2008). At the secondary level, high NaCl salt concentrations lead to ionic imbalance (often called as ionic stress) and nutritional imbalance (Kamanga and Mndala, 2019). Na^+ and K^+ compete for their binding sites as both have the same ionic radii and share similar transportation pathways. Therefore, resulting excess Na^+ deposition in the cytosol replaces K^+ ions required in some key biochemical reactions (Shrivastava and Kumar, 2015). The secondary damages, resulting from prolonged exposure, make changes in redox state that elicits the excessive generation of cellular entities (reactive oxygen species or ROS) (Abdelaziz et al., 2018; Nahar et al., 2016). ROS cause damage to essential cell constituents such as lipid membranes, proteins, DNA, and RNA, and thus causing aging and ultimately inducing cell demise (Mittler, 2017; Sameena and Puthur, 2021).

Interestingly, plants use innate defense mechanisms to scavenge ROS and maintain redox homeostasis. The increasing ROS upsurges a powerful and multifaceted antioxidant machinery that consists of enzymatic and non-enzymatic components. This efficient system helps in the scavenging of ROS by neutralizing and transforming them to non-toxic forms (Farooq et al., 2015; Liebthal et al., 2018). For regulating osmotic stress, plants enhance osmolyte biosynthesis which is probably universal and regulates osmotic adjustment, diminishes damage lead by ROS, prevents membrane injury, and stabilizes proteins and other enzymes (Hannachi and Van Labeke, 2018).

The major crops including both legumes and cereals rich in bulk of calories are glycophytes. However, when these crops are subjected to NaCl concentrations exceeding 200 mM, they are unable to survive (Flowers et al., 2015). Thus, improving salt tolerance in such crops is of great importance for global food security (Zhao et al., 2020). The overall effect will be inhibition of cell division, differentiation, and elongation that declines growth performance and results in the yield loss of plants. Moreover, the impact of salt stress and its tolerance range on several crops especially grain legumes are still obscure (Parihar et al., 2015).

This literature review primarily focuses on NaCl salt stress that is the wide and most significant abiotic stressor. The negative symptoms and common strategies to NaCl salt stress adopted by plants are described presently.

Overall impacts of salinity stress on plants

The rate of photosynthesis

All physiological processes depend upon photosynthesis since the diminished rate of photosynthesis brings negative impact on quantum yield. The outcome would be both diminished crop yield and quality of yield. Among chloroplast components, chlorophyll pigment constitutes a major part of photosynthesis and is an indicator of the quality of crops (Vakilian and Massah, 2017). The chlorophyll pigment and photosynthetic rate are positively correlated. However, reduced chlorophyll (Chl. *a*, *b*, and *Total*) and carotenoid contents might be linked with ROS toxicity led by excess salt ions deposition, with a consequence of destructed chlorophyll molecules and ceased uptake of essential elements including Mg, K, N, and thereby, enhanced activity of the chlorophyll degrading enzyme known as chlorophyllase (Bulgari et al., 2019; Sadak et al., 2020). Thus, growth reduction is a common phenomenon observed under high salinity (Bose et al., 2017), due to less availability of reducing potentials (ATP and NADPH) and N_2.

Besides, an inactivation of essential enzymes under high illumination required for Calvin cycle (second phase of photosynthesis) occurs. Interestingly, the reducing potentials formed by the phase-1 (light reaction) are used by the Calvin cycle to fix CO_2 for carbohydrate synthesis (Chu et al., 2015). However, stomatal closure brought on by salt stress reduces the amount of accessible CO2 (Lakra et al., 2018). Under such conditions, RUBISCO binds with available O_2, results in the production of 2-phosphoglycolate (Dellero et al., 2016). This 2-carbon compound inhibits two key enzymes involved in carbon metabolism and thus prevents the net rate of photosynthesis (Flügel et al., 2017). So, an efficient detoxification mechanism is needed in light-driven organisms (photosynthetic) to ensure the normal growth performance.

Kalaji et al. (2011) pointed out that inhibition of photosystem II (PSII) activity and thereby, diminishing photosynthetic efficacy in plants is a consequence of excess salt accumulation under salinity. Since, the target site of salt is PSII, this results in the blockage to electron carrier activity (Mehta et al., 2010), expansion of thylakoid membrane, and even disappearance of membrane. Moreover, chlorophyll content and electron carriers (ETC) display positive trend during light reaction (Hassannejad et al., 2020). Khan et al. (2010) reported salinity-induced reduction in photosynthetic efficacy of mung bean plants due to the decline in photosynthetic pigments and damage to electron carriers in PS-II. After irrigating wheat plants with sea water, Aldesuquy et al. (2014) also noted a 25% decline in physiological characteristics such as leaf area, Hill activity, and photosynthetic efficiency.

Plant growth, development, and *performance*

Salt stress affects every aspect of plant life from germination to reproduction stage. Salinity exposure results in delayed seed growth. Moreover, several crops show less tolerance to salinity at emergence stage and as a result reduced establishment is recorded (Maas and Grattan, 1999). Grattan et al. (2014) in cotton which is classified as “salt tolerant” noticed that the plant is sensitive to post germination stages and reduced plant densities have been found when fields were irrigated with saline water. Besides, salinity reduces growth-related characteristics including shoot and leaf area reduction, where the leaf size variation depends on mitosis and cell extension processes (Läuchli and Epstein, 1990). Undoubtedly, salinity causes reduction in cell numbers; however, leaf expansion, which is extremely affected by salinity, depends upon cell elongation (Munns and Termaat, 1986). Cell elongation processes are governed by cell wall extension phase and cellular water absorption, which in turn rely on the osmotic potential (Ψs) of the cell (Cramer and Bowman, 1993).

Moreover, Munns (1993) defined growth reduction under NaCl salinity as a two-phase system. In the initial phase (1), known as short term exposure, growth is affected due to cellular responses of osmotic effects while the latter (Phase 2) is characterized by prolonged effects when growth reduces due to accumulation of excess toxic salts. Furthermore, Schubert (2011) proposed the addition of a transient phase (Phase 0) prior to Phase 1, which is observed in salt shock scenarios. During this phase, plants show short-term changes like decline in turgor and growth rate that lasts minutes to hours after salt shock treatment. However, these changes are ephemeral and plants are able to get normal life after some time (Munns, 1993; Thiel et al., 1988).

Salt stress leads to inhibition of growth and thereby reduces yields in grain legumes (12-100%), which results chiefly from the suppression of morpho-physiological responses (Flowers et al., 2010; Khan et al., 2017). The diminished grain yield during stress is attributed to low pollen viability, stigma reception, and photo-assimilate transportation at grain filling stage. Nitrogen-based compounds such as proteins are the prime target of salinity-induced changes in cell (Negrão et al., 2017).

Higher salt deposition and reduction in growth-related traits have been recorded in mustard seedlings (Yousuf et al., 2017). Similar, negative symptoms of salt stress have een found in soybean fennel (Semiz et al., 2012), and pepper plants (Baath et al., 2017) cultivated in saline environment.

Tolerance mechanisms adopted by plants

Salt tolerance is defined as the potentiality of a plant to complete its life cycle in saline soil without having harmful effects over it. Normally, plants defend stress by bringing change in their cellular processes and interpreted them as an alarm signal. If this stress is tolerated hardening occurs. If the stress exceeds the tolerance range, cells get injured and finally plant dies.

Interestingly, roots are the first target organ that act as sensing and shield for soil-born stresses in plants. However, rhizosphere region affected by soil salinity can adversely hamper the growth of plants, as the roots cannot pullout water from the rhizosphere. Unlike, other salts like Ca^{2+}, K^{+}, Mg^{2+}, Cd^{2+}, etc, Cl^{-} ion(s) in the soil affect other vital elements needed for normal growth performance of the plant (Carmen and Roberto, 2011). Na^{+} is a micronutrient for plants and plays an essential role at low concentrations. However, excess sodium salts inhibits growth and biomass of roots, stems, and leaves (Chartzoulakis and Klapaki, 2000). High concentration of Na^{+} results in a change of pH and potential difference across the membrane. This causes the elimination of K^{+} from the cell and thereby disrupts normal cellular function.

On the other hand, different plants have adopted various responses and mechanisms of stress resistance such as synthesis of antioxidants, low molecular weight molecules known as osmolytes, and cellular ion balance. Tolerance rate depends upon the duration, stage, and genotype of plant species, which also varies between and within the species (Munns and Tester, 2008). Such changes provide information regarding identification of genes, their loci, and natural variations that are critical for abiotic tolerance in plants (Zhao et al., 2020). The role of defensive mechanisms against salinity stress are depicted in Fig. (I). All plant species, i.e., tolerant as well as sensitive displays plants that are subjected to an external stress, e.g. NaCl stress, display some degrees of tolerance towards stress. However, tolerant species show some sort of resistance over longer time under excess ROS condition. The three organelles including mitochondria, chloroplast, and peroxisomes are primary and major sites of ROS formation. NADPH oxidases is the basic pathway of ROS formation. Under optimal concentrations ROS (red solid arrow in Fig. I) act as signaling molecules in plants. The coordination of ROS and antioxidants serve as a defense line before stress as antioxidants keep ROS level under control by quenching and converting them into less harmful products (brown dotted arrow in Fig. I). This is observed in tolerant species and some sensitive species at low doses of stress over a specific time. However, when the stress level goes beyond the tolerance range, ROS blocks antioxidant machinery (round circle brown red dash line in Fig. I). As a consequence, signaling from the cell cytosol (right direction brown dotted arrow in Fig. I) activates cell growth protein inactivation. Subsequently, expression of senescence associated genes (SAGs) is activated, which results in a decline in expression of senescence down-regulated genes (SDGs). Finally, plants suffer

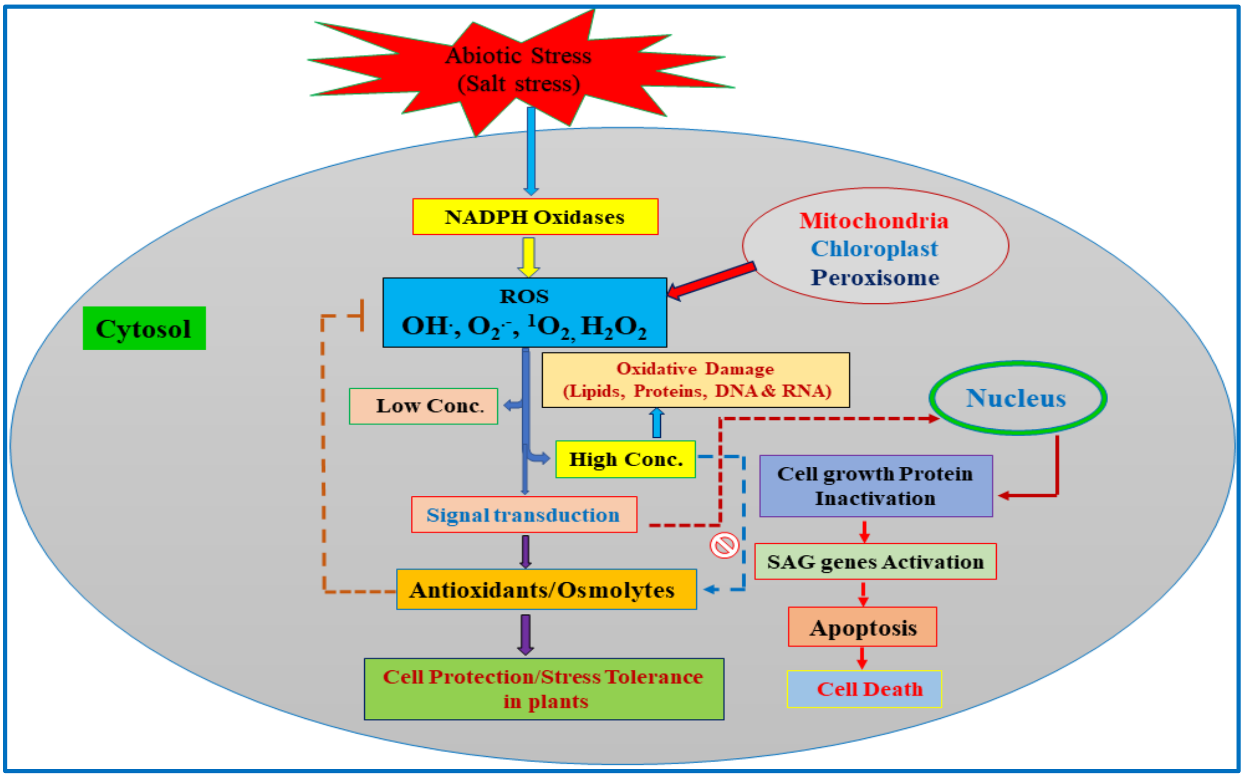

Fig. I. Regulation of defence mechanism by plants to tolerate salt stress

decline in metabolic activities, triggers apoptosis, and eventually dies.

ROS production sites and *their hallmarks*

The evolution of oxygenic atmosphere provides aerobic organisms and other energy producing systems with O_2, which is used as the final electron acceptor for normal cellular activities. However, molecular oxygen is unreactive, and its reduction leads to generation of reactive oxygen species (ROS). The four basic ROS are hydrogen-peroxide (H_2O_2), hydroxyl radical ($OH^{\cdot}$), superoxide radical ($O_2^{\cdot -}$), and singlet oxygen ($1O_2$) (Gill and Tuteja, 2010). The aerobic cellular processes lead to continuous ROS formation (1-2% of total consumed O_2) (Mittler, 2017), in which different pathways are involved, the main pathway being NADPH oxidases and peroxidases. In addition to this pathway, cellular compartments such as chloroplast, peroxisome, and mitochondria also play roles in ROS production (Mignolet-Spruyt et al., 2016). Formation of ROS plays dual role in stressed plants depending upon their concentrations. At low levels, ROS act as intracellular signaling agents and trigger different defensive systems against oxidative stress. However, excess concentrations of ROS are extensive and have capability of interacting with different organic molecules (RNA, DNA, proteins, and lipids), resulting in metabolic disorders, aging, and consequently cell demise (Ke et al., 2018; Sharma et al., 2012). The role of ROS defined as oxidants and redox signaling components depends on their balance between production and detoxification in subcellular organelles. Such toxic properties of ROS develop a detoxification mechanism in plants for maintaining normal cellular homeostasis (Kushwaha et al., 2019; Mittler, 2017).

Interestingly, plants possess a defense mechanism to scavenge ROS. For instance, antioxidants system includes enzymatic and non-enzymatic components that provides tolerance to external stress (Farooq et al., 2015). In saline environments, such enzymes work together in coordination to improve the performance of plants. Despite providing a solution for ROS, these enzymes' expression occurs in a time-bound manner. It also depends on the growth stages of the plants under stress conditions. The well-known mechanism called water-water cycle proposed by Asada (1999) explains how these antioxidants work together during the onset of oxidative stress. This cycle possesses a property of scavenging ROS $O_2^{\cdot -}$ anion and H_2O_2 at their production sites before their interaction with target molecules. Enhanced antioxidant levels and sodium chloride tolerance were reported in several crops including rice (Shao et al., 2015), cotton (Wang et al., 2016), and tomato (Kamanga et al., 2020).

Antioxidant machinery and salt stress tolerance

Superoxide dismutase (SOD) **(EC 1.15.1.1)**

One of the fastest enzymes is SOD with ($V_{max} = 2 \times 109\ M^{-1}S^{-1}$), an optimum close to the diffusion rate of $O_2^{\cdot -}$(McCord and Fridovich, 1969). The first conversion of $O_2^{\cdot -}$to H_2O_2 is the initial step in the enzymatic scavenging of ROS and SOD serves as a primary defense against oxygen radicals (del Río et al., 2018). It removes $O_2^{\cdot -}$radical and reduces the risk of OH^- formation via the metal cu/Fe catalyzed by Haber- Weiss type reaction (Fenton reaction), which is the most reactive reaction in the biological world. Since, the Haber-Weiss type reaction compared to spontaneous dismutation reaction is 10,000-fold faster, SODs are regarded as the first line of defense against stress in plants (Alscher et al., 2002).

$$O_2^{\bullet -} + O_2^{\bullet -} + 2H^+ \rightarrow 2H_2O_2$$

SODs is of three types based on the presence of required metal cofactors in cell organelles including chloroplast, peroxisome, and mitochondria. These three forms are FeSOD, MnSOD, and Cu/ZnSOD. Moreover, under stress conditions, different SOD isoforms have been observed in plants (Alscher et al., 2002). Regarding isoenzyme forms and their role in salinity stress, Eyidogan and Öz (2007) with *C. arietinum* noted three different SOD isozyme bands viz., MnSOD, FeSOD, and Cu/ZnSOD under salinity. Likewise, MnSOD isozyme overexpression in transgenic arabidopsis showed an increased salt tolerance (Wang et al., 2004).

In glycophytes, a positive and negative trend has been found between increased SOD activity and salinity stress tolerance (Maksimović et al., 2013). On the other hand, halophytes have a significant in born potential in utilizing SOD as defense against salinity stress damages. An upsurge in SOD activity under expanding NaCl-stress has previously been reported in *Panicum miliaceum* (Mir et al., 2019), common bean (Farhangi-Abriz and Torabian, 2017), rice cultivars (Frukh et al., 2020), and Chyosum (Kamran et al., 2020). These studies suggest SOD as a prime enzyme in shielding plants exposed to NaCl stress.

Catalase (CAT) **(EC 1.11.1.6)**

The catalyst for the dismutation of H_2O_2 into H_2O and O_2 is a tetrameric heme-containing protein called Catalase (Abdelaal et al., 2018). This was the first AOX enzyme to be discovered and functionally characterized. Additionally, the site of CAT enzyme is restricted to peroxisomes in all aerobic metabolisms. Due to β-oxidation of fatty acids, photorespiration, purine catabolism, and oxidative stress in plants, peroxisomes are the hot spots of H_2O_2 production (Mittler, 2002).

$$H_2O_2 \rightarrow H_2O + (1/2)\ O_2$$

Undoubtedly, CAT enzyme shows high specificity and the highest turnover rate for H2O2, i.e., conversion of 6×10^6 molecules of H2O2 to H_2O and O_2 min^{-1} (Gill and Tuteja, 2010). However, its activity is efficient only when H2O2 is present in higher amounts. The reason is its lower affinity for H2O2 than APX and other peroxidases (Mittler, 2002).

Based on different reports regarding catalase activity, it was observed that catalase behavior is related to plant species and environmental conditions. In addition, there is a great difference in published data about catalase activities. Indeed, some authors defended CAT's role in AOX defense system, whilst others opposed their role against environmental stresses as increased superoxide radical (O2$^{\cdot -}$) directly inhibits CAT activity (Kono and Fridovich, 1982). In support to this ROS inhibiting activity, several authors addressed reductions in the CAT activity led by oxidative stress (Iannone et al., 2015; Soares et al., 2018). Ashraf et al. (2018) observed higher enzyme levels in salt-treated plants in comparison to non-stress plants. Similarly, Sofy et al. (2020) found that CAT activity steadily enhanced in common bean plants treated with different levels of NaCl (50 mM and 100 mM).

Ascorbate peroxidase (APX) **(EC.1.11.1.11)**

Ascorbate peroxidase is an important enzymatic-antioxidant present in all plants and other organisms. It breakdowns H2O2 into water and monodehydroascorbate (MDHA) by using ascorbic acid (AsA) as a reducing agent (Desoky et al., 2019a; Sharma et al., 2012). Ascorbate peroxidase family is based on four different isoforms viz. thylakoid ascorbate peroxidase (tAPX), glyoxisome forms (gm APX), chloroplast stromal soluble form (sAPX), and cytosolic form (cAPX) (Noctor and Foyer, 1998).

$H_2O_2 + AA \rightarrow 2H_2O + DHA$

APX possesses some specific features over CAT which presents its significant role as antioxidant enzyme under abiotic stress. It shows high affinity for H2O2 catalysis and even performs better in scavenging of H2O2 present in low concentrations than CAT enzyme (located in peroxisomes only). Another feature of APX is that it shows its scavenging activity in cellular parts other than peroxisomes, e.g., cytosol and chloroplast. Increased levels of APX have been noticed with increased salt concentrations in common bean (Farhangi-Abriz and Torabian, 2017), two flax varieties (Mekawy et al., 2020), and rice cultivars (Frukh et al., 2020).

Osmolytes **and** *salinity stress*

Plants must lower their internal water potential in order to compensate for the decrease in external osmotic potential and sustain normal growth. Both the synthesis and accumulation of osmolytes as well as the absorption and accumulation of ions from the medium can result in osmotic adjustment. Although both processes are possible, the dominance of either one depends on the species and salinity levels.

Crop plants have adopted a common strategy to minimize the salt stress damages by a phenomenon known as osmoregulation, which takes place through ion uptake and organic solutes formation including L-proline, glycine-betaine, sugars, sugar alcohol, and trehsol (Farooq et al., 2015). Computable solutes are defined as “organic osmolytes characterized by their low molecular weight and high solubility, compatible with the cell’s metabolism, referring to protein interactions and stabilization of macromolecules, irrespective of species and stress type” (Hannachi and Van Labeke, 2018).

Accumulation of osmoprotectants in salinity is a metabolic adaptation, which defines primarily the turgor balance between the cytosol and vacuole. Among these quaternary amino acid compounds, glycine-betaine and free-proline are ubiquitous protein-stabilizing osmolytes that occur during varied stress conditions of plants (Mansour and Ali, 2017; Nahar et al., 2016). Others solutes including sugar alcohol (glycerol), complex sugars (trehalose, raffinose and fructans), and polyols also play roles in plants' adaptation to various stresses.

Proline (Pro)

L-proline is an important osmolyte that plays a diversified role under abiotic stress conditions in plants (Iqbal et al., 2019). Free proline biosynthesis involves two different pathways through glutamate and ornithine cycles, using glutamic acid and ornithine as substrates, respectively. The proline biosynthesis pathway known as glutamate pathway (main pathway) occurs either in the cytoplasm or chloroplast and is governed by two enzymes, namely ð1-pyrroline-5-carboxylate synthetase (P5CS, 1-2) and Pyrroline-5-carboxylate reductase (P5CR). But the change of L-proline back to an intermediate state called glutamate takes place in mitochondria only. This whole process is termed as “L-proline cycle” (Verslues and Sharma, 2010).

The upsurged proline content facilitates H_2O uptake and reduces ion toxicity in the cytosol, and thus prevents tissue damage in plants under continuous exposure to stress condition (Ashraf and Foolad, 2007; Mir and Somasundaram, 2020). In addition to these properties, L-proline plays a significant role during stress by acting as an antioxidative defense molecule and an amino acid (Barupal et al., 2019), signaling molecule, stress reliever, and plant development (Meena et al., 2019). The higher proline content during salinity stress helps in regulating turgor and ion homeostasis, thereby improving stress tolerance in plants (Kaur and Asthir, 2015; Mir and Somasundaram, 2020).

Despite such properties, a tremendous amount of energy is used by plants during osmotic adjustment. “An estimation of 30-50 molecules of ATP are required for synthesis of one osmolyte”. However, Na+ ion uptake is considered as a cheaper source than osmolytes in turgor adjustment as it consumes only 3- 4 molecules of ATP/mol (Raven, 1985). Interestingly, halophytes have such a potential for using Na^+ as a “cheap osmoticum” to maintain turgor and thereby, regulate stomatal operation and elongation growth. Because of this, they are able to safely sequester extra harmful Na+ and Cl- ions in the vacuole and keep their organellar and cytosolic concentrations below dangerous levels. In this way cytosolic osmotic potential is adjusted by upsurged organic osmolyte accumulation to match inorganic ions of the vacuole (Zhao et al., 2020).

Glycine betaine (GB)

Glycine betaine is a quaternary NH_4^+ molecule that regulates osmotic potential and ion efflux to help keep cell metabolism in check. As Malekzadeh (2015) put it, GB is an electrically neutral amphoteric compound at different pH with high solubility in water that allows it to interact with both hydrophilic and hydrophobic regions of macromolecules. Unlike halophytes, glycophytes belonging to family Poaceae only possess potentiality to biosynthesize and accumulate GB in their tissues as a response mechanism to external stresses such as salinity (Annunziata et al., 2019). However, this process is particularly observed in young leaves only during continuous exposure to stress, the reason being ontogenetic factors of plants (Annunziata et al., 2019).

Formation of GB takes place in the chloroplast stroma by choline oxidation or by N-methylation of glycine reactions (Chen and Murata, 2002). Its accumulation has been observed at significant levels in many salt-tolerant plants (Rhodes and Hanson, 1993) and salt tolerant blue-green algae to maintain osmotic potential (Chen and Murata, 2008). In addition, under high NaCl salt levels, betaine may also prevent light harvesting complex II (LHCII) protein damage (Papageorgiou and Murata, 1995). Rhodes and Hanson (1993) reported that higher GB levels are related to osmotic adjustment under dehydrating conditions of plants during extended salt stress.

Increased accumulations of GB may improve the function of protein complexes present in thylakoids and prevent membrane fluidity by changing the lipid composition of thylakoid membrane under stress (Williams, 1994). Such changes in the membrane composition and other properties are important factors of plant adaptability to salt environment (Russell et al., 1995). There is now strong evidence about the role of GB under various abiotic stresses. Deposition of GB in halophyte *A. griffithii* and its increase with rise of salinity was reported by Khan et al. (2000b). Glycine betaine was found to help in maintaining water status by osmotic pressure in *Prosopis alba* (Meloni et al., 2004) and protecting thylakoid membrane damage in wheat (Tian et al., 2017) under salinity stress. Sofy et al. (2020) noticed that GB doses markedly induced morpho-physiology and productivity of common bean when subjected to salinity stress. Similar positive results of alleviated GB levels have been noted in soybean and snap bean (Desoky et al., 2019b; Malekzadeh, 2015).

In conclusion, we can argue that GB and Pro play diversified role in plants by maintaining osmotic potential of a cell due to their amphoteric nature at earlier stages of salt stress. However, further study is needed to elucidate the role of such osmolytes in protecting plants under prolonged stress and thereby activating and/or accelerating antioxidant machinery to diminish ROS levels.

Stress sensing* and *signaling by subcellular organelles

Because of their sessile nature, plants must show resilience to abiotic stressors. Also, plants display some specific changes in their physiology, metabolism, and gene expression towards changing environmental stress conditions. This requires that plant cells have the capability of sensing various environmental signals using chemical hormones. The cell surface has specific proteins known as receptors that manage the perception and response to the external signals. The subcellular organelles have also specific receptors that play a vital role in sensing external signal and its response.

Stress perception is frequently controlled by ligand perception, which is located at the cell membrane. In order to get a specific signal response to the external factor or stress, this signal is then transferred to several subcellular sites, including the nucleus. Endoplasmic reticulum stress (ER stress), or alternations in protein folding brought on by stress, is a recognized crucial physiological response to stressful situations. Stress also interacts with other cellular organelles, and the signals produced by each organelle in response to stress are combined to control the production of genes that respond to stress and other cellular processes, thus resorting cellular equilibrium. Their role as sensors are briefly described in the following sections.

Cell-Wall Stress

The basic cell wall is made up of cellulose fibrils embedded in a pectin gel, joined by hemicellulose tethers such as xyloglucans and arabinoxylans (Tenhaken, 2015). The wall also includes phenolics, pectin esterases, peroxidases, other wall losing enzymes called expansins, and Ca^{2+} that helps to stabilize and extend cell wall during growth. Osmotic stress treatments like NaCl salt leads to ROS accumulation that causes crosslinking of such polymers, resulting in the cell-wall stiffening. However, stress can regulate the expression of modifying enzymes taking part in expansins and xyloglucan to remodel the wall (Tenhaken, 2015). Additionally, cell wall integrity plays a crucial role in determining how well *Arabidopsis* plants tolerate salt stress and thrive (Zhao et al., 2018). For instance, Wsc1-3, Mid2, and Mtl1 are proteins that sense cell wall stress in yeast. These proteins are referred to as wall-associated plasma-membrane proteins (Jendretzki et al., 2011). It is unknown, however, how such sensors identify cell-wall deformations. However, their ability to serve as mechanosensors is aided by the existence of a sizable O-mannosylated extracellular domain that is rich in serine and threonine residues. The two proteins that connect the cellulose synthase complex to microtubules and play a crucial role in plant growth under salt stress were recently identified by Endler et al. (2015).

Endoplasmic reticulum (ER) stress

The main cause during stress is the protein unfolding sensed as ER stress, the results of biotic and abiotic factors (Zhao et al., 2020). Specific ER membrane sensor proteins are able to detect this type of stress, which expresses genes encoding stress proteins known as chaperones. Such chaperone genes prevent unfolding of proteins during stress time. Further, unfolded protein response (UPR), a conserved stress response in eukaryotes, is a part of their expression that aids in restoring ER homeostasis (Walter and Ron, 2011). Liu and Howell (2016), reported two different proteins of ER involved in ER stress, namely ER membrane-associated transcription factor and RNA splicing factor. The ER stress expresses the plasma-membrane associated NAC transcription which in turn helps to support UPR. In addition to functioning as ER stress agents, the leucine zipper proteins bZIP28 and bZIP17 also interact with the chaperone protein known as "binding immunoglobulin protein". The second kind of IRE1 protein senses ER stress by attaching to improperly folded proteins. This causes splicing of bZIP60 mRNA, resulting in a bZIP60 variant form that enters the nucleus and thereby activates UPR genes and finally confers stress tolerance (Liu and Howell, 2016).

Chloroplast stress

Chloroplast is the organelle present in the mesophyll of leaves and in some green parts of plant, where photosynthesis and other chemical reactions happen. Although, it is a semi-autonomous organelle containing its own genetic machinery, still metabolic balance is easily disturbed by abiotic stressors. It is considered a major site for ROS production under stress (Mignolet-Spruyt et al., 2016). Additionally, in plants under stress, coordination between the chloroplasts and the nucleus is crucial. This calls for an ongoing flow of transmission from the organelles known as retrograde signaling from the chloroplast to the nucleus (de Dios Barajas-López et al., 2013). Further, three different routes are involved in this signaling pathway viz. (1) Intermediates of tetrapyrrole biosynthesis, (2) transcriptional and translational processes impairment in organelles, and (3) changes in redox status in chloroplast and accumulation of $^1O_2$ and H_2O_2 (Galvez-Valdivieso and Mullineaux, 2010).

Formation of singlet oxygen ROS in the grana or lamellae of chloroplast has a critical role in signal transduction pathway by involvement of two nuclear encoded proteins including EXECUTER1 (EX1) and EXECUTER2 (EX2). Thus, changing nuclear gene expression results in chlorosis and cell death in wild type. However, no such changes were found in ex-mutants in Arabidopsis (Wagner et al., 2004). Furthermore, both EX1 and EX2 directly play roles in sensing singlet oxygen. Along with EX1 and EX2, singlet oxygen-led signal also happens independently through-carotene breakdown products, which aids in salt tolerance (Ramel et al., 2012).

Peroxisome and *mitochondrion stress*

Like chloroplast stress in plants, retrograde signals generated by mitochondria and peroxisomes are crucial for the transmission of stress. Such organelles are sources of essential metabolites and ROS, some of which act as retrograde signals (Ng et al., 2014). In addition, mutation or dysfunction of mitochondrial "DEXH box RNA helicase" results in ROS formation and accumulation. Such ROS lead to change in responses of a stress hormone called ABA in plants (He et al., 2012). Similarly, CHY1 mutations cause ROS formation and decline chilling tolerance by impairing chilling response gene expression.

Ion homeostasis, transport, and molecular adaptive responses by plants

Salinity stress is usually associated with too much NaCl present in the soil. Because Na^+ ion deposition is considered to be toxic, most research focuses on revealing the mechanisms of Na+ transport and its sequestration in plants (Zhao et al., 2020). Two main effects of salt stress on plants are osmotic impact and availability of soil water extraction. Osmotic effect results from greater levels of soluble salts in the rhizosphere. The second impact is increased salt accumulation within cell compartments, which leads to ion toxicity. Disruption of metabolic processes, including the inactivation of several enzyme activities necessary for photosynthesis, is the overall result (Munns and Tester, 2008). However, ion toxicity is a very significant consequence of saline stress, and the severity of this effect is determined by ion transport and accumulation in various plant parts, tissues, and cells (Roy et al., 2014).

Negative symptoms of salinity in plants can be mediated and reduced by three steps related to ion balance. The first step involves blockage of Na + ion transport to shoots through apoplastic barriers including casparian bands and suberin lamellae. The second stage is the dilution of Na^+ ion by transporting them to vacuole from cell cytosol. The third step is the exclusion of Na^+ ion outside the cell by involvement of an antiporter known as plasma membrane Na^+/H^+ antiporter (Byrt et al., 2014). These changes are seen at all phases of plant life (Kalaji et al., 2018). However, at the physio-biochemical level, plants possess several defensive mechanisms that can help them to differ or alter electron flow during photosynthesis to defend themselves against stress (Feng et al., 2014).

However, The ion homeostasis between Na^+ and K^+ is essential for normal growth and can be gained through ion uptake that regulates cell osmotic pressure (Hasegawa, 2013). Intracellular Na^+ and K^+ balance not only plays a role in various enzymes activities, but also is needed for balancing membrane potential and cell volume. NaCl is a common salt in the soil and the most common stress is seen by excess toxic concentrations of Na^+ and Cl^- ion(s) in the soil. Therefore, in order to lessen the impacts of salinity on crops a thorough study is needed to understand the Na^+ ions transport across the membrane and its compartmentalization. On the other hand, the specific transport mechanism in charge of bringing sodium chloride into the cell is unknown.

Physiological data indicates that Na^+ competes with K^+ for intracellular influx since having similar hydrated ionic radii of Na^+ and K^+ results in Na^+ toxicity in cells, and they are also bound and carried by common transporter proteins (Blumwald et al., 2000). Another factor is that Na^+ ions act as a low energy vacuolar osmolyte in saline environments.

Interestingly, several strategies and/or mechanisms have been involved in plants to provide stress tolerance against excess Na^+ and Cl^- ion accumulations. Such mechanisms include replacement of Na^+ ion by K^+ ion, Na^+ exclusion, and retention of intracellular K^+ (Nahar et al., 2016). Despite their similarity in physiochemical properties, potassium ions show higher binding affinity than Na^+ at the plasma membrane and tonoplast channels (Rubio et al., 2020). Moreover, K^+ takes part in cell signaling process by driving a "metabolic switch" to inhibit energy dependent biosynthetic processes. These metabolic changes during salt stress result in counteracted Na^+ ion concentrations. Finally, reduction in growth results in storage of energy and utilizes this energy in enhancing plants' capacity to synthesize compounds to defend and repair damage of cellular systems during stress condition (Demidchik et al., 2014). Interestingly, no such an elucidated mechanism to block the Na^+ ion(s) passage or complete exclusion of Na^+ relative to K^+ in various cell compartments of plants are obsderved.

Schroeder et al. (2013) reported that some plant membrane transporters play a key role in stress resistance mechanism especially Na^+ and K^+ transporters. Roots exist multiple Na^+ influx pathways including plasma membrane. However, some channels and transporter mutants have the capability to block partial passage of Na^+ entry in the cell. For instance, calcium-permeable non-selective cation channels (NSCCs) (Hua et al., 2003) and Glutamate-like receptor (GLR) families (Tapken and Hollmann, 2008) allow Na^+ ions and represent gateway for Na^+ ions in the cell. Na^+ entry in above ground parts of plants takes place mainly by efflux out from stellar cells. The potential candidates that control Na^+ loading in xylem vessel are the outward-rectifying K^+ and KORC and NORC channels.

The energy-transducing membranes of chloroplast and mitochondria contain large, multiprotein ATPase complexes. Such $\mathrm{ATPases}$ are known as F-type $\mathrm{ATPases}$ because they utilize the energy associated with membranes to drive ATP synthesis. However, ATPase complexes found at the plasma membrane and vacuolar membrane of cells are called ATPase-proton pumps $(\mathrm{H}^+ - \mathrm{ATPase}$ as they work in opposite manner, i.e., rather than synthesizing ATP such $\mathrm{ATPases}$ hydrolyze ATP, they use negative free energy to ''pump'' protons across the membrane against an electrochemical gradient. The vacuolar membrane possesses two different H^+- pumps, an H^+- ATPase type vacuolar pump $(\mathrm{V} - \mathrm{ATPase})$ and a vacuolar pyrophosphatase pump $(\mathrm{V} - \mathrm{Ppase})$ (Dietz et al., 2001). However, V-ATPase pump shows more significance in plant survival under harsh climatic conditions (Dietz et al., 2001). Thus, excess sodium being transported in the vacuole provides an effective mechanism for avoiding sodium symptoms (Farooq et al., 2015). The vacuolar $\mathrm{H}^+ - \mathrm{ATPase}$ and $\mathrm{H}^+ - \mathrm{Ppase}$ activity in tonoplast membrane of salt tolerant soyabean variety enhanced relatively compared with moderately tolerant variety (Yu et al., 2005)

Salt oversensitivity (SOS) protein signaling pathway

The discovery of salt oversensitivity (SOS) signaling pathway was a milestone in NaCl stress physiology to understand how plants deal with salt load. Furthermore, this pathway also provided a clear mechanism of Na^+ exclusion from the cytoplasm to the exterior of cell (Zhao et al., 2020). To lessen the effects of Na^+ toxicity under saline conditions, plant cells have a tendency to efflux toxic Na^+ or isolate Na^+ ion(s) in the vacuole, in order to build new ion homeostasis. The SOS family represents three genes namely (SOS 1, 2, and 3), which together form a critical SOS signal transduction pathway during salinity in plants (Chinnusamy et al., 2005). SOS1 consists of an Na^+/H^+ channel protein with 10-12 trans-membrane proteins domains. The Na^+/H^+ antiporter (SOS1) helps to maintain low cytosolic Na^+ by exclusion process (Zhu, 2003). In addition, SOS1 has three functions, namely (i) Na^+ efflux from cytoplasm to the rhizosphere, (ii) providing time gap for Na^+ accumulation in the vacuole by slowing down Na^+ deposition in the cytosol, and (iii) controlling long-distance Na^+ transport between roots and shoot through Na^+ retrieval.

The Ser/Thr protein kinase also known as SO2 consists of two domains, i.e., regulation domain at C-terminal and a catalytic domain at N-terminal, both being activated by the Ca^{2+} signals stimulated by salt stress (Liu et al., 2000). SO3 is a myristoylated Ca^{2+} binding protein having a place for the myristoylation on its N-terminal. This N-terminal position plays a major function in salinity stress tolerance (Shi et al., 2000). The SOS2 and SOS3 interaction activates protein kinase and in turn, phosphorylates SOS1 protein, enhancing its transport activity. Guo et al. (2004) also reported that overexpression of SOS1 or SOS2 protein may improve salt tolerance in plants.

Interestingly, any mutation in the SOS pathway leads to enhanced sensitivity of the plant to salt. Therefore, to prevent cytoplasm from its toxicity, transporting sodium in the vacuole is a vital and efficient strategy in plants to tolerate salinity. Similar to bacteria and fungi antiporter, expression of the gene AtSOS1, which codes for the plasma membrane Na^+/H^+ antiporter, causes NaCl resistance in Arabidopsis (Shi et al., 2000). In rice plants *nhaA* of *E. coli* encodes Na^+/H^+ antiporter improved salinity tolerance (Wu et al., 2005). Likewise, *AVP1* overexpression in encoding vacuolar H^+-pyrophosphatase results in salt tolerance of Arabidopsis and cotton plants. Liu et al. (2011) identified a gene called *ScVP* from *Suaeda corniculate*. This gene encodes a vacuolar H^+-pyrophosphatase $(\mathrm{V} - \mathrm{H}^+ - \mathrm{PPase})$ and confirms salinity tolerance in Arabidopsis. Moreover, expression of vacuolar (AVP1) gene in cotton plants confers abiotic stress tolerance.

Conclusion

Among abiotic stresses, salinity is a serious issue in view of the increasing population worldwide. This is due to the shrinkage of arable land and increasing anthropogenic activities. Exposed to adverse environmental conditions, staple crops exhibit a common response, i.e., ROS generation. ROS, the byproduct of aerobic respiration, are found to play a bi-functional role in plants. Low ROS serve as a signaling agent of damage in plants while their overexpression triggers stress-signaling components to prevent further damages led by oxidative stress and observed maximum in mitochondria and chloroplast. Plant cells possess a defensive mechanism (antioxidants and compatible solutes), which maintains ROS-induced oxidative stress. Despite their role in stress tolerance, proline and GB as antioxidants need to be readdressed. This might help in future to replenish AOX action, where they fail to persist over longer time. Research to improve salinity tolerance and generate salt tolerant plants to curb food crisis in future needs to delve into the way signaling pathways take place between organelles and their pivotal role as stress sensors in saline condition.

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