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REVIEW

Salt Stress Induced Plant Physio-biochemical and Molecular Responses: A Review

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Salt stress-induced limitation in crop growth and produce is a critical problem worldwide. The prerequisite to developing salt-tolerant plants of commercial importance is understanding the plant responses to salinity exposure at physiological, biochemical, and molecular levels, integrating various approaches to understanding underlying salt tolerance mechanisms, and utilizing naturally occurring genetic resources available for salt tolerance. In this review, plant responses and associated salt tolerance, at physiological and biochemical levels through ion homeostasis, osmolyte accumulation, hormonal regulation, antioxidant responses, and mitogen-activated protein kinase cascade signaling and molecular responses through transcription factors, different gene expressions, non-coding RNA production, and epigenetic modifications are presented.

Key words: Epigenetic modifications, ion homeostasis, non-coding RNA, salinity tolerance, transcriptional factors

A broad spectrum of abiotic stresses like acidity, alkalinity, salinity, and microbial infections are harmful to the plants. Salinity stress is among the most crucial environmental stresses to the productivity of crops worldwide (Flowers 2004; Munns and Tester 2008). Soil salinity shows a high concentration of soluble salts in the soil moisture of the rhizosphere. According to the United Nations Environment Programme, nearly 50% of the world's cultivated land is saline (Flowers and Yeo 1995). Salt stress in plants can occur in two ways; first, high soil salt concentration makes it difficult for roots to absorb water, and second, the high content of salt within the plant may prove fatal as it is toxic (Munns and Tester 2008). Saline stress in plants may hamper the various processes such as flowering, fruit quality, seed germination, survival percentage, which leads to decreased crop productivity (Sairam and Tyagi 2004). Severe consequences of salinity on plant growth may be because of ion toxicity in cell and osmotic stress (Hussain *et al.,* 2007). Lipids are major constituents in the cell membrane, which help to maintain cell tolerance to saline stress. Increased saline levels disturb the arrangement of lipids and proteins in the cell membrane, which leads to defective lipid metabolism (Guo *et al.,* 2019). The most challenging circumstance for salt stress is the degradation of chlorophyll content, which terminates photosynthesis level in plants, and it also hampers the stomatal conductance, respiration rate (Doganlar *et al.,* 2010).

The initial reaction shown by salt-stressed plants is water potential decrease, which hampers water use efficiency, resulting in significant toxic damage and reduced yield (James *et al.,* 2011). Water relations and osmotic adjustment regulate salt-stressed plants' growth responses (Munns *et al.,* 1983). Salinity stress inhibits water content in many crop yielding plants such as pea, tomato, Mentha, balm, showing a deleterious reduction in crop yield (Ozturk and Unlukara 2004). Metabolic adjustments in response to salinity stress are dynamic and multifaceted, e.g., under salt stress, the most dramatic change occurs in the ice plant (Guan *et al.,* 2020). Salt stress can bring out a shift from C_3 to CAM pathway in this succulent plant by the induction of some enzymatic machinery, e.g., Phosphoenolpyruvate (Romano *et al.,* 2020) carboxylase, within a few hours, and the transition occurs within 6 to 8 days. The striking feature of CAM plants is scotoactive stomata, by which they can use water efficiently by showing minimum transpiration rate (Guan *et al.,* 2020).

Some metabolic changes are common to most plants, whereas others are specific, e.g., organic solutes of low molecular weight show salt-stress induced accumulation. These solutes comprise amino acids (proline or glutamate), betaines (glycine betaine and alanine betaine), and polyols. During nitrogen deficiency, plants usually accumulate sulfonium compounds, like dimethyl-sulfonium propionate, which are physiologically similar to nitrogen-containing betaines. These organic solutes act antagonistically to inorganic solutes like Na and Cl ions, even at high concentrations, and are not detrimental to the enzymes and cell organelles. That is why these organic compounds preferentially function as compatible osmolytes (Rhodes and Hanson 1993; Ashraf and Harris 2004). Studies revealed that higher plants could tolerate high salinity by exclusion or accumulation of salt. Salt excluders have the property to remove salts from the whole plant or particular organs. In such situations, membrane permeability supports the intake of K^+ over Na+. Thus, the crops which exclude salts are distinguished by the low concentration of Na^+ and Cl^+ ions (Chen *et al.,* 2018). Salt accumulators possess the ability to uptake high salt content through the following two mechanisms. In the first mechanism, plants can withstand high concentrations of intercellular salts by tolerant cell membranes, a common feature of salt-stressed plants, e.g., Halophytes. In this way, the ratio of Na^+ to K^+ in tissues is apparent. The second mechanism involves eliminating excess salt that enters the plant, from which roots can uptake ions to prevent their detrimental effects (Yensen 2006).

Salt tolerance through physiological and biochemical mechanisms

Salt stress negatively affects plant growth through various constraints like osmotic stress, wherein water uptake by plants is affected, triggering significant events like the arrest of the shoot and root (Munns *et al.,* 2000; Fricke *et al.,* 2004). Therefore, the osmotic adjustment becomes the requirement for plants in such conditions. Though reduced, the root growth rate resumes within an hour by regaining cell turgor by inorganic ions uptake and changing cell wall composition like Na+ binding affecting Na^+ passage and other ion bindings (Shabala and Lew 2002; Byrt *et al.,* 2018). The assimilation of CO_2 is also affected by osmotic stress through the rapid closing of stomata, resulting from reduced xylem pressure. The roots sense and send the hydraulic signals at fast speed while shoots transduce these signals immediately to alter its metabolism, and ion channels in guard cells decode the altered xylem pressure to alter stomatal conductance (Furuichi *et al.,* 2008; Christmann *et al.,* 2013; Shabala *et al.,* 2016).

Salt stress-induced ion toxicity, mostly related to increased Na^+ and Cl^- accumulation, also restricts plant growth. Na^+ toxicity lethal effect on plants though unknown can occur through enzyme inhibition; for example, many enzymes functioning in primary metabolism, regulated by $K^{+,}$ get inhibited through the replacement of K^+ by Na^+ (Wu *et al.,* 2018). Salt sensitive plants exhibit increasing physiological dysfunctions with increasing shoot Cl^-levels; thus, salt tolerance demands the exclusion of Cl^- from shoots (Geilfus 2018; Teakle and Tyerman 2010). Halophytes can withstand Cl^- concentration more than 1M without any adverse effect, and Cl^- affects the plant by causing less availability of macronutrients like S and N, as Cl^- share the anion transporters with SO_4^{2-} and NO_3^- (Bazihizina *et al.,* 2019). Salt stress, mostly Na^+ specific, cause PCD (programmed cell death) in plant roots, and events like cytochrome c release and DNA fragmentation occur rapidly (Jiang *et al.,* 2008). Mutants of *Arabidopsis* lacking GORK, a K^+ channel, show reduced or no such PCD events, suggesting entry of Na^+ into cytosol causes membrane depolarisation, K^+ efflux, activation of PCD executing endonucleases, and caspase-like proteases (Demidchik *et al.,* 2010; Demidchik 2014).

Ion Homeostasis

NaCl is the primary soil salinity stress determinant, so the mechanisms underlying Na^+ transport and its sequestration have remained the researcher's primary focus. The accumulation of a high concentration of Na^+ in the root cell cytoplasm is prevented by excluding Na^+ from uptake and vacuolar compartmentalization of Na^+ (Theerawitaya *et al.,* 2020) . Na^+ uptake by roots is carried by various ion transporters in which two essential types include non-selectively operating cation channels, HKT2 (high-affinity K^+ transporters), and CNGCs (cyclic nucleotide-gated) or GLRs (glutamate receptor-like) (Demidchik 2018; Mian *et al.,* 2011). Other suggested transporters involved in Na^+ uptake include HAK5, AKT1, LCT1 (low-affinity cation transporter1), and PIP2-1 (aquaporins) (Schachtman *et al.,* 1997; Mian *et al.,* 2011; Isayenkov and Maathuis 2019; Kronzucker and Britto 2011; Byrt *et al.,* 2017). The counterbalance of Na^+ uptake occurs through Na^+ expulsion through SOS1 Na^+/H^+ exchanger and vesicles, and about 95% Na^+ returns to the rhizosphere (Shi *et al.,* 2002b; Shabala *et al.,* 2020). Na^+ vacuolar sequestration is done by Na^+/H^+ tonoplast antiporters of the NHX family, which show elevated transcript levels and activity in glycophytes upon salt exposure and constitutive activity in halophytes (Bassil and Blumwald 2014; Shabala and Mackay 2011). Two types of leak channels in tonoplasts, SV and FV (fast), need to be tightly regulated to block the leakage of Na^+ back into the cytosol (Shabala *et al.,* 2020). Further, Na^+/H^+ antiporter's higher affinity for K^+ than Na^+ suggests the operation of other mechanisms like vacuolar trafficking in delivering Na^+ to the vacuole (Bassil *et al.,* 2019; Baral *et al.,* 2015). The loading of Na^+ into xylem occurs both actively and passively, and the importance of mode of uptake depends on the time after salt exposure (Ishikawa *et al.,* 2018b). NSCC mediate the passive Na^+ xylem loading while SOS1 Na^+/H^+ antiporter and HKT2 (K^+/Na^+ symporter) carry the active loading (Guo *et al.,* 2010; El Mahi *et al.,* 2019; Jabnoune *et al.,* 2009). SOS1 Na^+/H^+ antiporter occurs abundantly in xylem parenchyma and HKT2 in stellar tissues of the root. Saline conditions favour passive K^+ outward movement from parenchyma cells into the xylem due to depolarization, which creates a driving force for Na^+ xylem loading (Ishikawa *et al.,* 2018b). The CCC (cation-chloride cotransporters), which mediate K^+, Cl^-, and Na^+ symport, create a driving force by transporting Cl^- into the xylem passively, for active Na^+ xylem loading (Ishikawa *et al.,* 2018a). HKT1 (Class I) transporters remove Na^+ from xylem sap, and these transporters are more selective for Na^+ than K^+ (Munns *et al.,* 2012). Also, Na^+ is recirculated back to the roots from the shoots through the phloem involving mainly HKT1, and this Na^+ gets stored in stellar parenchyma cells to prevent phototoxicity and damage to shoot meristematic tissues and growing leaves (Kobayashi *et al.,* 2017; Shabala 2017).

Osmolytes and Osmoprotection

Osmolytes, compatible solutes or osmoprotectants are polar, soluble, uncharged, and chemically varied organic compounds, not interfering with cellular processes even if accumulated at high concentrations. These include glycine betaine, proline , polyols, sugar, hydroxyproline, β-alanine, polyamines, and LEA (late embryogenesis abundant) proteins (Tahir *et al.,* 2012; Wang and Nii 2000; Kerepesi and Galiba 2000; Saxena *et al.,* 2013). Different plant species show variations for amounts of organic osmolytes synthesized and accumulated, like proline accumulated in varied plant groups, whereas β-alanine is accumulated only in some members of plumbaginaceae (Saxena *et al.,* 2013; Hanson *et al.,* 1994). The external osmolarity determines the osmolyte accumulation, and thus through water influx, osmolytes function in the protection of structures and maintenance of cell osmolarity (Hasegawa *et al.,* 2000).

The quaternary ammonium compounds that physiologically act as potent compatible plant osmolytes under salt stress are glycine betaine, (β)-alanine betaine, proline betaine, choline-O-sulphate, hydroxyproline betaine, and pipecolate betaine (Ashraf and Harris 2004). GB shows ubiquitous occurrence in organisms like cyanobacteria, bacteria, fungi, algae, animals, and several families of plants like families Chenopodiaceae and Gramineae over an extensive range of abiotic stress conditions (Turkan and Demiral 2009; Lokhande and Penna 2012). This osmolyte is mostly found in chloroplasts and plays a significant role in stromal adjustment and thylakoid membrane protection, and hence and photosynthetic activity is maintained (Jagendorf and Takabe 2001). PS-II (photosystem II) complex is protected by GB in saline conditions (Annunziata *et al.,* 2019). Against osmotic stress, GB prevents the membrane and enzyme (like Rubisco) destabilization induced by heat (Giri 2011). In angiosperms, synthesis of GB within the cell occurs from choline via ethanolamine, by two sequential oxidation reactions catalyzed by enzymes, namely CMO (choline monooxygenase) and BADH (betaine aldehyde dehydrogenase) respectively (Luo *et al.,* 2012a; Missihoun *et al.,* 2015). In some plants, another biosynthetic pathway involving two N-methyl transferase enzymes shows GB synthesis from glycine (Ahmad *et al.,* 2012). Studies revealed that GB improves salt tolerance in maize, tobacco, potato, rice, barley, tomato belonging to different agronomical crops. The exploitation of these plants in biotechnology for GB synthesis has provided tolerance against various abiotic stresses (Sairam and Tyagi 2004; Turkan and Demiral 2009). GB's unique structure enables it to interact with macromolecules like enzymes through hydrophilic and hydrophobic domains. It functions in stabilization of proteins, osmotic adjustment, prevention of damage to photosynthetic apparatus, and lowering ROS (Reactive Oxygen Species) levels (Ashraf and Foolad 2007; Saxena *et al.,* 2013; Cha-Um and Kirdmanee 2010). Pre-treatment of rice seedlings with GB can prevent damages like grana disintegration, thylakoid swelling, mitochondrial swelling, and foliar spray of GB, leading to increased photosynthetic rate, pigment stabilization, and enhanced growth (Rahman *et al.,* 2015; Ahmad *et al.,* 2012).

In contrast to other amino acids like methionine, arginine, and cysteine, which show a decreased concentration, proline shows an increase in concentration under salt stress (El-Shintinawy and El-Shourbagy 2001). The accumulation of proline (Liu *et al.,* 2006) provides a measure of improvement of salinity stress, and its intracellular accumulation serves as a nitrogen reserve for after recovery utilization (Saxena *et al.,* 2013; Ben Ahmed *et al.,* 2010). The Pro concentration is metabolically regulated, and synthesis of this imino acid occurs in plastids and cytoplasm, while it is broken down to L-glutamate (Kadioglu *et al.,* 2012) in mitochondria. In plants, Pro has two precursors viz; glutamate (Kadioglu *et al.,* 2012) and ornithine (Orn). Pro synthesis occurs from Glu via glutamic – Ƴsemialdehyde and pyrroline-5-carboxylate (P5C). The conversion of Glu to P5C is catalyzed by P5C synthase (P5CS) succeeded by P5C reductase (P5CR), which reduces P5C to Pro (Ashraf and Foolad 2007). Pro-biosynthesis also takes place from another precursor Orn which is transaminated to P5C with the involvement of an enzyme mitochondrial Orn –Ɣ-aminotransferase (Ong *et al.,* 2016; Verbruggen and Hermans 2008). Pro biosynthesis is negatively regulated by a bHLH TF, MYC2, by limiting the expression of P5CS (Verma *et al.,* 2020). Pro can quench $^1O_{2,}$ act as a free radical scavenger, buffer cellular redox potential, and mitigate cytoplasmic acidosis under stress (Babiychuk *et al.,* 1995; Matysik *et al.,* 2002; Lee *et al.,* 2008). In *Olea europaea*, proline supplements improve salt tolerance by enhancing enzymatic antioxidants, photosynthesis, osmotic balance, and plant growth, while in tobacco, it enhances salt tolerance through the acceleration of antioxidant defence pathway-specific enzymatic ac under stress (Babiychuk *et al.,* 1995; Matysik *et al.,* 2002; Lee *et al.,* 2008). Inlular structures like proteins and membranes are stabilized by Pro through cluster formation with water, thereby preventing their denaturation, and membranes are protected through the maintenance of cellular ion homeostasis and osmotic balance (Ashraf and Harris 2004; Lee *et al.,* 2008; Gleeson *et al.,* 2005). Silicon supplementation increases the Pro content 3 to 6 days and decreases it 9 to 12 days after salt exposure and negative correlation between Pro and cytokinin exist after 3 days of stress, suggesting communication between cytokinin and Pro metabolism. Silicon induced Pro increase that can regulate cytokinin to confer salt tolerance (Zhu *et al.,* 2020c)

Sugar and Sugar Alcohols:

The correlation between salt tolerance and fluctuations in soluble carbohydrate concentrations shows that the accumulation of carbohydrates like sugars (fructose, sucrose, glucose) and starch occurs due to salt stress (Parida and Das 2005). At higher salinity (400-500 mM NaCl), plants like *Cakile maritime* and *Aster tripolium* accumulate more elevated amounts of total soluble carbohydrates and proline (Megdiche *et al.,* 2008; Geissler *et al.,* 2010). Sugar alcohol and sugars function in storing carbon, scavenging radicals, osmoregulation, and osmoprotection (Ahmad and Sharma 2008; Lee *et al.,* 2008; Adams *et al.,* 2005). Furthermore, there is deliberation about the sugar and sugar alcohols as molecular chaperones (Liu *et al.,* 2006; Hasegawa *et al.,* 2000). In *Setaria sphacelata,* starch and sugar show reduction in amounts under water stress for the short-term while soluble sugars increase and starch decrease in long-term stress, suggesting a metabolic shift towards sucrose because starch turnover is more affected than sucrose (da Silva and Arrabaca 2004).

Trehalose, a non-reducing sugar, helps angiosperms protect from abiotic stress and alleviates salt-induced oxidative stress by preventing ROS accumulation (Mostofa *et al.,* 2015). Salt tolerance increases in transgenic rice overexpressing OsTRE1, a trehalase gene (Islam *et al.,* 2019). While functioning as osmoprotectant and osmolyte, it prevents membranes and proteins from undergoing denaturation (Ashraf and Harris 2004). Transgenic plants exhibit a reduction in photo-oxidative damage and increased photosynthetic rate with increased trehalose levels under salt stress. It protects biological molecules from injuries induced by desiccation through its potential for water absorption and in maize seedling growth improved via regulation of the glyoxalase system and antioxidant by trehalose through a reduction in ROS, methylglyoxal, malondialdehyde, and Na+/K+ (Rohman *et al.,* 2019; Penna 2003). Sugar alcohols (Polyols) can be acyclic like mannitol or cyclic polyols like pinitol, having multiple functional OH-groups, and act as osmolytes, ROS scavengers, and chaperones (Ashraf and Foolad 2007). These can work as osmolytes in osmotic adjustment and osmoprotectants through two indistinguishable means, and osmotic adjustment occurs through the facilitation of cytoplasmic water retention and apoplast or vacuolar Na^+ sequestration (Parida and Das 2005). Accumulation of polyols in grapes under water deficit conditions provides a means for refining water use efficiency and grapevine practices (Conde *et al.,* 2015).

Polyamines

Polyamines or organic amines, including Spd (spermidine), Put (putrescine), and Spm (spermine), increase salt tolerance when applied exogenously, or their levels increased in transgenic plants (Bueno and Cordovilla 2019; Rathinapriya *et al.,* 2020; Ji *et al.,* 2019). Different stresses induce polyamines that regulate the functioning of specific ion channels to control ionic influxes and play a protective role, as evidenced by the outcome of exogenous application (Zhao *et al.,* 2007; Pottosin and Shabala 2014). Transgenic overexpression and loss of function mutants support polyamine's protective role (Ji *et al.,* 2019; Zarza *et al.,* 2017). The endogenous level of plant polyamines increase after salt exposure, and polyamine catabolism regulates the endogenous level and the oxidative catabolism catalyzing enzymes of polyamines, amine oxidases, are essential in imparting salt tolerance (Takahashi and Kakehi 2010). Polyamines maintain membrane integrity, regulate gene expression governing osmolytes' metabolism, reduce ROS production and control Na^+ and Cl^- accumulation in various plant organs (Ji *et al.,* 2019; Rathinapriya *et al.,* 2020; Seo *et al.,* 2019). Spermidine and spermine, when exogenously applied to like in soybean seedlings, enhance photosynthesis and ROS metabolism, thereby improve growth and enhance salt tolerance (Wang and Yin 2014; Baniasadi *et al.,* 2018). SAMDC (S-adenosylmethionine decarboxylase) upregulation and ODC (ornithine decarboxylase) and ADC (arginine decarboxylase) downregulation led to decreased Put and increased Spm and Spd accumulation, alleviating the salt-induced inhibition of growth (Takahashi *et al.,* 2017). Spd and Spm affect many metabolic pathways, and in grape seedlings, polyamines with ABA alleviate salt stress (Paul and Roychoudhury 2017; Sun *et al.,* 2018). ADC2 deletion increases salt sensitivity, whereas ADC expression leads to enhanced osmotic adjustment and better plant growth (Naka *et al.,* 2010; Espasandin *et al.,* 2018).

LEA Proteins

Late embryogenesis abundant proteins occur in plants and animals that prevent desiccation, protein aggregation, or osmotic stresses (Furuki *et al.,* 2012; Hundertmark *et al.,* 2012; Hand *et al.,* 2011). Named after their finding in maturing seeds, constitutive expression, or salinity stress-induced expression of LEA proteins are reported (Cumming 1999; Liu *et al.,* 2013). LEA proteins protect various plant molecular or cellular structures from damaging effects of H2O2 through hydration, buffering, ion sequestration, direct protection of membranes or other proteins, or unfolded protein renaturation and phosphorylation is supposedly to have an enormous impact on the functioning of LEA proteins under stress conditions (Zhang *et al.,* 2000; Goyal *et al.,* 2005; Liu *et al.,* 2017). IpLEA, gene product from Ipomoea pes-caprae, belonging to LEA group 2 functions in drought and salt tolerance through the facilitation of water homeostasis or ROS scavenging (Zheng *et al.,* 2019). LEA group 1 proteins (XsLEA1-8) in Arabidopsis thaliana, while avoiding damage to subcellular structures, enhance the drought and salt tolerance (Artur *et al.,* 2019). LsEm1 (LEA group1), from lettuce, when overexpressed in rice, alters the expression of other genes like OsCDPK25, OsCDPK15, OsCDPK13, OsCDPK9, and rab21 positively leading to increased salt and drought tolerance (Xiang *et al.,* 2018). CaDHN5 (Luo *et al.,* 2019) overexpression upregulated several salt-responsive genes, increasing osmotic and salt tolerance (Luo *et al.,* 2019).

HORMONAL REGULATION OF SALINITY STRESS

Many phytohormones like ethylene, GA, ABA, jasmonic acid (JA), and salicylic acid coordinate and integrate, enabling plants to respond and adapt to salt stress while ABA among these acts in different abiotic stresses. Water deficit and osmotic stress induced by salt stress result in rapid ABA production in shoots and roots (Shi *et al.,* 2002b). ABA binding to receptors like RCAR (REGULATORY COMPONENTS OF ABA RECEPTORS), PYL (PRY1-LIKE), and PRY1 (PYRABACTIN RESISTANCE1) leads to inhibition of PP2C phosphatases and promotion of SnRK2s activity that can activate many anion efflux channels resulting in turgor pressure loss and stomatal closure (Duarte *et al.,* 2019; Zhang *et al.,* 2017). Previously ABA was thought to be produced in roots exposed to osmotic stress and regulate stomatal closure; however, evidence like upregulation of gene NCED3 encoding enzyme in leaf parenchyma upon osmotic stress, catalyzing the first step of ABA biosynthesis, suggest ABA delivery to shoot from roots is not necessary (Endo *et al.,* 2008; Buckley

2019). Besides, synthesizing ABA in roots would require precursor transport from leaves (Zhang *et al.,* 2018). The role of ABA produced in roots under salt stress is still unclear even though ABA produced in roots has a higher concentration than leaves (Shi *et al.,* 2002a). ABA in osmotically stressed roots stimulates NADPH oxidase that induces H2O2 production and accumulation, triggering stomatal closure and thus provides a clue of its role in salt stress response (Nath *et al.,* 2019). OsABAR1 encoding GRAM (glucosyltransferases-like GTPase activators and Myotubularin) protein positively regulates the ABA pathway and enhances tolerance to salt and drought through ABA (Zheng *et al.,* 2020).

Several JA biosynthesis genes upregulate by salt stress, suggesting the role of JA signaling in salt stress-induced plant responses (Kazan 2015; Geng *et al.,* 2013). Salt stress inhibits root elongation through JA signaling. Physical interaction of RSS3 (RICE SALT SENSITIVE3) protein with class C bHLH (basic-helix-loop-helix) TFs (transcription factors) and JAZ (JASMONATE ZIM_DOMAIN) proteins induce cell elongation whereas RSS3 mutants show enhanced expression of JA-responsive genes, suggesting JA functions in root growth inhibition under salt stress (Toda *et al.,* 2013). GaJAZ1 affects salt tolerance in cotton through downregulating genes containing G-box cis-element and reprogramming of defence associated gene expression (Zhao *et al.,* 2020). OsCYP94C2b gene, encoding an enzyme catalyzing the conversion of jasmonoyl isoleucine (active form) to the inactive one, when overexpressed, increases the chances of survival in rice, suggesting JA regulates salt tolerance negatively. Though, TaORP1, the gene for JA biosynthesis, overexpression, or JA exogenous application, result in enhanced salt tolerance, suggesting positive regulation of salt tolerance by JA (Kang *et al.,* 2005; Dong *et al.,* 2013). GA (Gibberellic acid) plays a critical role in plant growth regulation under stress conditions, and endogenous GAs reduce while DELLA proteins increase in seedlings on exposure to salt stress (Colebrook *et al.,* 2014; Magome *et al.,* 2008). DELLA proteins mediate salt-induced growth restriction and help plants survive (Achard *et al.,* 2006). GA deficiency *in vivo* enhances salt tolerance through Na^+ sequestration in vacuoles and ROS homeostasis (Zhang *et al.,* 2020f). Ethylene is vital in imparting salt tolerance as evidenced by increased salt tolerance by applying ACC (1-aminocyclopropane-1-carboxylic acid), the precursor of ethylene, and salt hypersensitivity due to mutations in genes involved in ethylene signaling (Cao *et al.,* 2007; Peng *et al.,* 2014). Ethylene positively regulates salt tolerance by modulating ROS scavenging and generation pathways (Peng *et al.,* 2014).

SA enhances the osmoprotectant (glycine betaine, polyamines, proline) accumulation and enzymatic antioxidant activities under salt stress, suggesting its positive role in conferring salt tolerance (Misra and Misra 2012). SA induces salt tolerance by the restoration of membrane integrity and increased carotenoid and chlorophyll content, resulting in enhanced accumulation of soluble sugar and K^+ in the root (El-Tayeb 2005). Increased antioxidant metabolism and enhanced sulfur and nitrogen assimilation promoted by SA lead to an increased photosynthetic reduction (Nazar *et al.,* 2011). SA treatment enables plants to adapt under saline conditions by reducing NaCl promoted H^+ influx and K^+ efflux (Jayakannan *et al.,* 2013). BR (Brassinosteroid) increase antioxidant enzyme (GPX, APX, POX, and SOD) activity and lead to the accumulation of tocopherol, reduced glutathione, and ascorbate (non-enzymatic antioxidants), thereby alleviating adverse salinity effects (El-Mashad and Mohamed 2012).

Antioxidant responses of salinity tolerance

ROS, mostly hydroxyl radical (OH^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and singlet anion ($O_2^{.-}$), show an increased production under different environmental stresses, including the salt stress and mitochondria, chloroplasts, peroxisomes, and apoplast are their main sites of generation (Miller *et al.,* 2010). NADPH oxidases AtRbohF and AtRbohD, polyamine oxidase, diamine oxidase, and peroxidase mediate the apoplastic ROS production, and salt stress leads to the upregulation of AtRbohF and AtRbohD genes, whereas plant mutant atrbohF/artboarD exhibit salt hypersensitivity (Ma *et al.,* 2012). Salt induced ROS production by AtRbohF/AtRbohD leads to cytosolic K^+ influx resulting in decreased Na^+/K^+ ratios. AtRbohF restricts xylem Na^+ distribution, thereby hampers Na^+ transport from root to shoot, whereas AtRbohD helps in the propagation of environmental stimuli induced long-distance signal (Miller *et al.,* 2009; Jiang *et al.,* 2012). Salt induced antioxidative response against H_2O_2 production mediated by AtRbohF/D helps decrease cellular oxidative damage (Ben Rejeb *et al.,* 2015). The chloroplast is the primary singlet oxygen and hydrogen peroxide producer compared to other organelles (Davletova *et al.,* 2005). During photosynthetic electron transport, the photoreduction of O_2 to O_2^- takes place and is termed as Mehler Reaction. In the plastoquinone pool, the formation of superoxides is due to the reduction of molecular oxygen. In PS-I during ETC, this reduction is executed by plastosemiquinone, ferredoxin, or by sulfur redox centres (Dat *et al.,* 2000). The conversion of superoxides to H_2O_2 occurs either naturally or by enzyme SOD action, and the hydroxyl radicals are produced from hydrogen peroxide (Pospisil *et al.,* 2019). In plant cells, peroxisomes are the leading producers of intracellular hydrogen peroxide, and H_2O_2 production induced by high oxygen and low CO_2 levels under salt stress enhance photorespiration (Wingler *et al.,* 2000; Del Rio and Lopez-Huertas 2016). The sites for O_2^- production in peroxisomes are peroxisomal matrix and peroxisomal membrane. In the peroxisomal matrix, the generation of O_2^- radicals occurs through xanthine and hypoxanthine oxidation to uric acid by enzyme xanthine oxidase (Gutteridge and Halliwell 2000). Salinity induces ROS production ($O_2^{\cdot-}$) in mitochondria through ubiquinone over-reduction leading to the release of electrons from the electron transport chain to oxygen (Miller *et al.,* 2010).

Plants use low ROS levels as signals to regulate growth and development in response to different stresses, whereas higher ROS concentration under stress conditions like salt stress has harmful effects. ROS disrupts cell integrity and leads to membrane lipid peroxidation, protein denaturation, pigment breakdown, damage to DNA and enzymes, and carbohydrate oxidation (Groß *et al.,* 2013). ROS activates various ion channels like Ca^+ channels sensitive to H_2O_2 in guard cells and root epidermal cells, Na^+ cation channels, K^+ efflux channels, Ca^{2+} pumps sensitive to OH^-, disturbing ionic homeostasis (Demidchik 2018; Zepeda-Jazo *et al.,* 2011). Plant ROS scavenging machinery detoxify the oxidative stress triggered by high salinity induced ROS accumulation, and ROS homeostasis maintenance plays a critical role in salt tolerance (Bose *et al.,* 2014). ROS scavenging induced salt tolerance includes both the activity of enzymatic antioxidants like SOD (superoxide dismutase), (Groß *et al.,* 2013) glutathione reductase, CAT (catalases), and APX (ascorbate peroxidase) and non-enzymatic antioxidant (glutathione, ascorbate, tocopherols) accumulation (Hanin *et al.,* 2016). Enhanced glutathione levels in chloroplasts, peroxisomes, and mitochondria increase, whereas reduced ascorbate levels, as in *vtc2-1*mutant, decrease salt tolerance (Bose *et al.,* 2014; Koffler *et al.,* 2015). Salt stress impairs the anthocyanin production, as seen in *air1* (*anthocyanin-impaired-response1*) mutant, evidencing the role of anthocyanin accumulation in salt tolerance (Van Oosten *et al.,* 2013). Glutathione acts as a ROS scavenger through its reaction with H2O2, superoxide, and hydroxyl radicals, and while acting in the ascorbate-glutathione cycle, it helps in the regeneration of ascorbate (Foyer *et al.,* 1997). In *Allium cepa*, exogenous application of glutathione restores the cell viability and plasma-membrane permeability under salt stress, and ascorbate plus glutathione application resulted in increased plant height and branch number and increased content of phenols, carbohydrates, mineral ions, and xanthophylls (Aly-Salama and Al-Mutawa 2010) (Rawia *et al.,* 2011). Ascorbate, an important antioxidant, mitigates the harmful impacts of salt stress and helps in plant recovery after salt stress exposure (Agarwal and Shaheen 2007; Munir and Aftab 2011). Plants can synthesize a lipophilic antioxidant known as alpha-tocopherol or Vit. E. In combination with other antioxidants, alpha-tocopherol scavenges free radicals (Munne-Bosch and Alegre 2003; Massacci *et al.,* 2008). It plays a crucial role in protecting the structure and function of PS-II as it chemically combines with oxygen in the chloroplast (Lopez-Huertas *et al.,* 2000). Alpha-tocopherol assists in membrane stabilization and mitigates tolerance of plants during oxidative stress (Munne-Bosch and Alegre 2003). Overexpression of OsVTE (encoding tocopherol cyclase in rice) IbTC (encoding tocopherol cyclase in sweet potato) enhanced the salt tolerance, and such a plant showed less accumulation of H_2O_2 (Ouyang *et al.,* 2011; Kim *et al.,* 2019). Superoxide anion is converted to H_2O_2 by SOD and H_2O_2 to water by APX in chloroplasts, and APX gene overexpression leads to enhancement in salt tolerance (Asada 2006; Badawi *et al.,* 2004). Under salinity stress, the activity of SOD increases in *Catharanthus roseus* and *Morus alba* (Jaleel *et al.,* 2008; Ahmad *et al.,* 2010). In mitochondria, Mn-SOD (manganese SOD) and alternative oxidase (AOX) increase salt tolerance through ROS detoxification (Giraud *et al.,* 2008). In rice, two isoforms of chaperone protein, NCA1a, and NCA1b interact mutually exclusive with CAT to control its activity and confer salt tolerance (Liu *et al.,* 2019a).

MAPK signalling cascade and salt stress

Over the period, plants have developed various mechanisms to counter and overcome the stress conditions for their survival, and among these mechanisms, signaling pathways, production, and shifting of signal molecules are crucial. Signal molecules are the by-products of biochemical reactions received by plant receptors, usually found in the cellular membrane, resulting in different gene expression, including stress genes, and help the plants tolerate and survive under stress conditions (Hamel *et al.,* 2006; Colcombet and Hirt 2008). Various signaling pathways get triggered during stress conditions, including MAPK (mitogen-activated protein kinase) signaling cascade. MAPK components are a group of enzymes that enable plants to respond to various stimuli by different stresses and activate plant responses like the activation of antioxidant enzymes. MAPK components get triggered by the activation loop's phosphorylation or dephosphorylation by upstream kinases, and phosphatases can suppress such activation (Lee *et al.,* 2009). Arabidopsis genome exhibits the ability to activate 5 MKP molecules, which include IBR5, PHS1, DSPTP1, AtMKP1, and AtMKP2. Among these molecules, AtMKP2 and DSPTP1 can dephosphorylate *Arabidopsis* MAPK molecules (MPK3,4, and 6) in-vitro, and MAPK component activation, and the expression of stress genes may increase plant response to stress (Lee and Ellis 2007).

The main MAPK molecules which get activated during stress are MPK6, MPK4, and MPK3, and under salt stress, M2K2 activates MPK4 (Colcombet and Hirt 2008). The upregulation of M2K2 and downregulation of MPK4 and MPK6 through MAPK cascade is related to Me2K (Teige *et al.,* 2004). In *Arabidopsis*, AtMPK6, AtMPK4, and AtMPK3 are regulated by salt stress, whereas salt stress results in MAPK's (ZmMPK5, ZmMAPK3, and ZmSIMK1) expression in corn (*Zea mays*) (Droillard *et al.,* 2002; Droillard *et al.,* 2004; Ding *et al.,* 2009; Wang *et al.,* 2010). Accumulation of ZmMPK3 RNA occurs in plants by treating it with ethylene, salicylic acid, hydrogen peroxide, ABA, or under salinity stress (Wang *et al.,* 2010). In *Arabidopsis*, ZmSIMK expression enhances plant salt tolerance (Kong *et al.,* 2011). StMAPK3 regulates salt and osmotic tolerance through affecting the activities of enzymes like CAT, SOD, peroxidases, and concentration of Pro, H_2O_2, and malondialdehyde (Zhu *et al.,* 2020b). In *Arabidopsis*, overexpression of the AtM2K3 gene increases plant tolerance to salinity and its sensitivity to ABA, implicating the signalling role of AtM2K3 in ABA activation and plant tolerance under salinity (Hwa and Yang 2007). In salt-tolerant peppermint, MAPK signaling regulates essential oil biosynthesis under salt conditions (Li *et al.,* 2016). Wheat MAPK phosphatase, TMKP1, when overexpressed, increases germination rates, enhanced antioxidant activities like SOD, CAT, and peroxidases, leading to salt tolerance enhancement (Zaidi *et al.,* 2016). In *Populus trichocarpa*, overexpression of MAPK kinase (PtMAPKK4) results in improved germination, growth, and tolerance.

Salt responses at the molecular level: gene expression and transcriptional regulation

Gene expression in plants is regulated through varied mechanisms resulting in specific gene expression under specific conditions. Salt stress-induced differential expression of thousands of genes is determined by salt exposure duration or strength (Zeller *et al.,* 2009). Transcriptome analyses of plants after salt stress alone or combined with other stresses propose widespread crosstalk between signaling pathways of salt stress and other stresses (Rasmussen *et al.,* 2013). TFs (transcription factors) constitute important regulators controlling gene expression, and TFs from prominent TF families like ERF/AP2, NAC, bZIP, WRKY, MYB act in salt response. SlMYB102, R2R3-type MYB TF overexpression confers salt tolerance through lowering ROS generation, K^+/Na^+ ratio maintenance, decreasing electrolyte leakage, enhancing the activity of SOD, CAT, APX, and peroxidase, increase in Pro, glutathione, and ascorbate concentrations, and upregulating several stress-associated genes like SICPK3, SICPK1, SIHAK5, SINHX4, SINHX3, SISOS2, and SISOS1 (Zhang *et al.,* 2020e). AtMYB49 (R2R3-type MYB TF) increases salt tolerance through changes in cutin deposition, elevating Ca^{2+} level and through upregulating genes for LEA and peroxidases, improving antioxidant capacity (Zhang *et al.,* 2020c). Another MYB TF, VcMYB4a in *Vaccinium corymbosum,* is suggested an essential abiotic stress repressor as its overexpression leads to enhanced salt sensitivity (Zhang *et al.,* 2020a).

Upregulation and downregulation of bZIP genes occur in salt-sensitive and salt-tolerant wheat cultivars, respectively, when exposed to an extended period of salinity, whereas in rice and wheat, NAC overexpression leads to salt tolerance (Johnson *et al.,* 2002; Nakashima *et al.,* 2007). LpNAC13 acting oppositely regulates drought tolerance negatively and salt tolerance positively, and its overexpression results in increased chlorophyll and proline content, increased enzymatic antioxidants and decreased malondialdehyde content under salt stress, whereas opposite results are found under drought conditions (Wang *et al.,* 2020b). CBF (C-repeat binding factor) from the AP2/ERF family plays a positive role in the salt response, as evidenced by an increase in salt tolerance by overexpressing CBF3/DREB1A (dehydration responsive element binding protein 1A) and salt hypersensitivity in mutants of CBF genes (Zhao and Zhu 2016; Kasuga *et al.,* 1999). DREB2, DREB1/CBF, and AREB/ABF TFs regulate abiotic stress responses transcriptionally, and TFs, ZFP179, and OsNAC5, are suggested to regulate the accumulation of LEA proteins, sugar, and proline under salinity stress, thereby conferring salt tolerance (Mizoi *et al.,* 2012; Fujita *et al.,* 2013; Song *et al.,* 2011). NnDREB2C overexpression in salt-stressed *Arabidopsis* increased germination, chlorophyll content, survival rates, lowered conductivity and resulted in increased tolerance to salt and drought through upregulation of PIP (Plasma membrane intrinsic proteins) genes (Ziyuan *et al.,* 2020). OsSTAP1 encoding AP2/ERF TF overexpression enhances salt tolerance through increasing activities of CAT, POD, and SOD, lowering Na^+/K^+ ratios and upregulating stress associated genes like peroxidase and other ERF encoding genes, suggesting its positive regulation of salt tolerance (Wang *et al.,* 2020c). AtWRKY8 in *Arabidopsis* shows increased expression and binds directly to the target gene RD29A promoter under salt stress (Hu *et al.,* 2013). IbWRKY2 enhances salt and drought tolerance in sweet potato through content increase for Pro and ABA, activity increase for SOD, and lowering H_2O_2 and malondialdehyde content (Zhu *et al.,* 2020a). SlWRKY28 in *Salix linearistipularis* is found to improve tolerance to alkaline salt stress by regulating genes involved in the pathway of ROS scavenging (Wang *et al.,* 2020a).

Regulation of gene expression by ABA mostly occurs through the bZIP TF subfamily, AREB/ABF, like ABF2 overexpression, enhances plant tolerance to multiple stresses (Choi *et al.,* 2000; Kim *et al.,* 2004). High salt and ABA hypersensitivity are exhibited by plants overexpressing DIG (Dynamic Influencer of Gene expression)/DIL (DIG-like), ABA-responsive TFs (Song *et al.,* 2016). MYC2, TF involved in jasmonate signaling positively regulates salt tolerance, and EIN3 TF involved in ethylene signaling enhances salt tolerance via DELLA proteins (Zhao *et al.,* 2014; Peng *et al.,* 2014). EIN3 act through ESE1 (Ethylene and Salt Inducible1) and ERF1 (Ethylene Response Factor1) and activate salt responsive gene expression (Cheng *et al.,* 2013; Zhang *et al.,* 2011a). SERF1 (SALT-RESPONSIVE ERF1) directly binds to MAPK6, MAPK5, ZFP179 (ZINC FINGER PROTEIN179), and DREB2A promoters and confers salt tolerance (Schmidt *et al.,* 2013). Some TFs can be controlled by different kinases that function in salinity tolerance like OsRMC encoding a receptor kinase that negatively regulates salt tolerance, is downregulated through binding of its promoter by two TFs, OsEREBP1 and OsEREBP2 (Serra *et al.,* 2013). Also, OsEREBP1 expression is not affected by ABA, salt, or severe cold but is regulated by moderate cold and drought slightly while ABA, cold, salinity enhance OsEREBP2 expression and drought, evidencing the role of OsEREBP2 in salt tolerance (Serra *et al.,* 2013). OSBZ8, a bZIP TF, in rice activated by phosphorylation through the SNF-1 group of serine/threonine kinase, is expressed highly in salt-tolerant than the salt insensitive cultivars (Gupta *et al.,* 2012). CaSBP12 (SBP-box TF) negatively regulates the salt tolerance through modulation of ROS signaling (Zhang *et al.,* 2020b).

Plant processes, mainly under various stress conditions, are influenced by alternative splicing. Alternative splicing regulating proteins like Ser/Arg rich proteins can splice alternatively under salt and other abiotic stresses (Staiger and Brown 2013). In *Arabidopsis*, alternative splicing involves the symmetrical demethylation of Arg side chains by Type II Arg methyltransferase, PRMT5, and *prmt5* mutants are salt sensitive (Zhang *et al.,* 2011b). PRMT5 alters H4R3sme2 (H4 arginine3 symmetric demethylation) and LSm4 methylation status and impacts the salt response and plant growth (Zhang *et al.,* 2011b). Salt, ABA, and mannitol upregulate the At-SKIP (Ski-interacting protein) expression, and altered tolerance of At-SKIP antisense lines or At-SKIP overexpressing lines in response to different stresses suggests the role of alternative splicing in such phenotypic expressions (Staiger and Brown 2013; Lim *et al.,* 2010). In *Arabidopsis*, nuclear SUMO proteases, OTS1 (Conti *et al.,* 2008) and OTS2 redundantly regulate salt stress responses, and the UBC32 (Ubiquitin conjugase) component of ERAD (endoplasmic reticulum-associated protein degradation) affect salt tolerance through BR (Cui *et al.,* 2012; Conti *et al.,* 2008). The existence of a mutual regulation mechanism between various signals, proteins, and genes is suggested to control various processes specific to abiotic stress adaptability of plants such as *in-vitro* salt tolerance increases when β-carotene hydroxylase downregulation leads the increased level of total carotenoid and β-carotene (Kim *et al.,* 2012).

Regulation of salt tolerance in plants is also influenced through epigenetic modifications like acetylation, methylation, ubiquitination, and phosphorylation. Many HATs (histone acetyltransferases) that catalyze histone acetylation and HDACs (histone deacetylases) that catalyze histone deacetylation function in salinity stress response such as HDA6 interaction with HD2C results in repression of ABI1 and ABI2 (ABA-responsive genes), thereby decrease salt tolerance (Luo *et al.,* 2012b). Salt tolerance is positively regulated by HDA5,14, 15,18 (class II enzymes), and negatively regulated by HDA6, 9, 19 (class I enzymes) belonging to the RPD3 family of histone deacetylases (Ueda *et al.,* 2017). HUB2 (E3 ligase from *Arabidopsis*) enhances salt and drought tolerance through increasing the monoubiquitination of H2B histone (Zhou *et al.,* 2017; Chen *et al.,* 2019). GmMYB84 encoding a TF conferring salt tolerance in soybean depends on DNA methylation, and upstream 690nt to 950nt of its initiation codon, DNA methylation level decreases upon salt exposure leading to its higher expression (Zhang *et al.,* 2020d).

Non-coding RNAs like miRNAs (microRNAs), siRNAs (small interfering RNAs), and lncRNAs (long non-coding RNAs) also mediate salt tolerance. miR-393 and miR-169 are induced, whereas miR-398 is inhibited by salt stress (Sunkar *et al.,* 2012), and miR319 induces salt tolerance through the downregulation of essential genes involved in the methionine cycle and upregulating genes for ethylene synthesis (Liu *et al.,* 2019b). A 24-nt nat-siRNA induces salt tolerance by downregulating the expression of enzyme P5CDH (delta1-pyrroline-5-carboxylate dehydrogenase), thereby inhibiting proline degradation (Borsani *et al.,* 2005). DRIR (Drought Induced lncRNA) regulates salt tolerance by modifying the expression of multiple genes (Qin *et al.,* 2017) and lncRNA973 in cotton increases salt tolerance through the regulation of TFs, salt-stress responsive genes, and ROS scavenging genes (Zhang *et al.,* 2019).

Stress priming or utilizing previous stress memory to enhance stress response by plants involves epigenetic modifications, inherited through mitosis or meiosis, like histone methylation and DNA methylation (Eichten *et al.,* 2014). Salt and drought tolerance increase through seed priming using hyperosmotic reagents or NaCl (Sani *et al.,* 2013; Cayuela *et al.,* 1996). With mild seed priming using salt, the H3K27me3 (histone H3 lysine 27 trimethylation) islands get shortened and fractioned, which results in an alteration in the transcriptional responsiveness of many genes upon second stress exposure (Sani *et al.*, 2013).

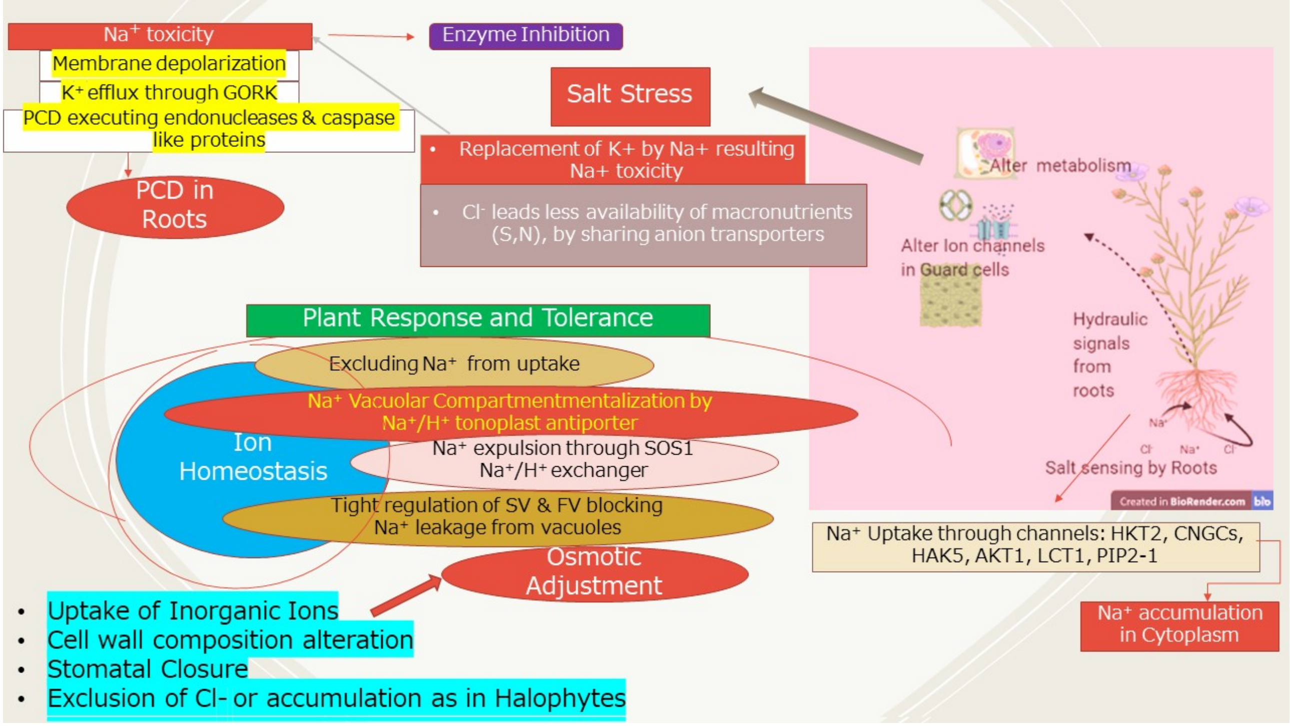
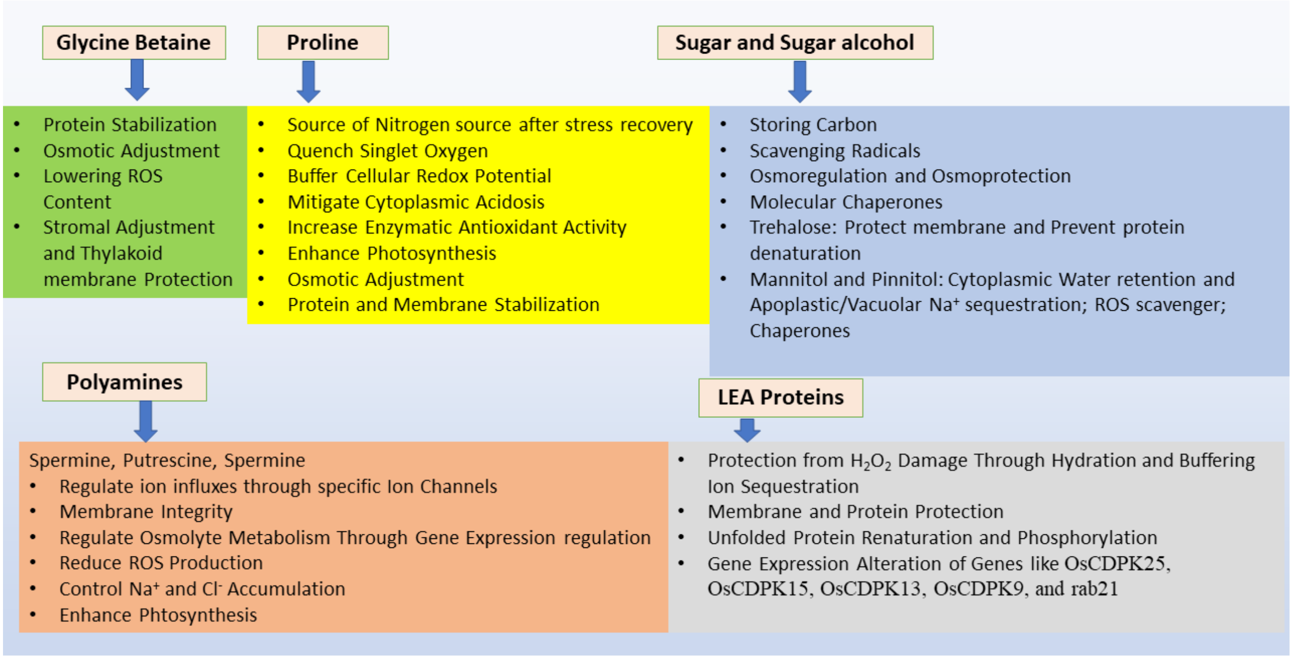


Figure 1: Figure representing Plant response and tolerance to NaCl



Glycine Betaine

- Protein Stabilization
- Osmotic Adjustment
- Lowering ROS Content
- Stromal Adjustment and Thylakoid membrane Protection

Proline

- Source of Nitrogen source after stress recovery
- Quench Singlet Oxygen
- Buffer Cellular Redox Potential
- Mitigate Cytoplasmic Acidosis
- Increase Enzymatic Antioxidant Activity
- Enhance Photosynthesis
- Osmotic Adjustment
- Protein and Membrane Stabilization

Sugar and Sugar alcohol

- Storing Carbon
- Scavenging Radicals
- Osmoregulation and Osmoprotection
- Molecular Chaperones
- Trehalose: Protect membrane and Prevent protein denaturation
- Mannitol and Pinnitol: Cytoplasmic Water retention and Apoplastic/Vacuolar Na^+ sequestration; ROS scavenger; Chaperones

Polyamines

Spermine, Putrescine, Spermine

- Regulate ion influxes through specific Ion Channels
- Membrane Integrity
- Regulate Osmolyte Metabolism Through Gene Expression regulation
- Reduce ROS Production
- Control Na^+ and Cl^- Accumulation
- Enhance Phtosynthesis

LEA Proteins

- Protection from H_2O_2 Damage Through Hydration and Buffering Ion Sequestration
- Membrane and Protein Protection
- Unfolded Protein Renaturation and Phosphorylation
- Gene Expression Alteration of Genes like OsCDPK25, OsCDPK15, OsCDPK13, OsCDPK9, and rab21

Figure 2: Role of osmolytes under salinity stress

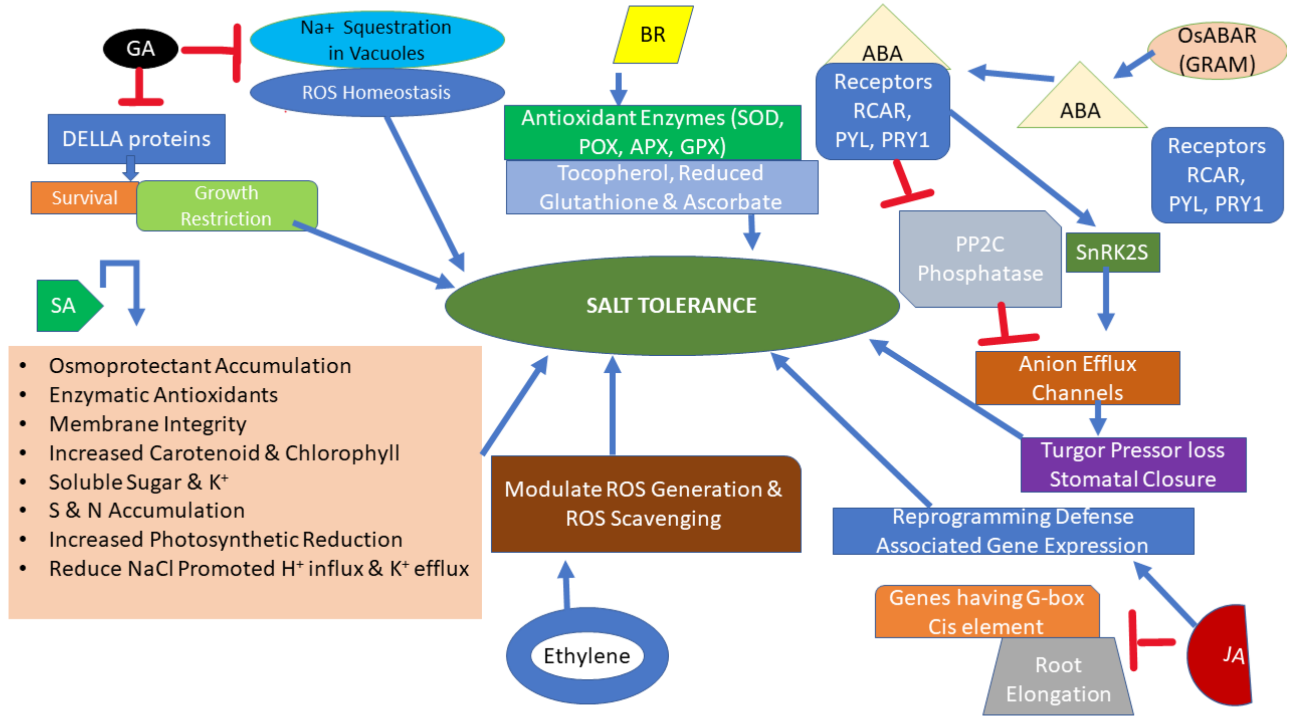


Figure 3: Role of phytohormones in imparting salt tolerance [GA (Gibberellic Acid), BR (Brassinosteroid), ABA (Abscisic Acid), SA (Salicylic Acid), JA (Jasmonic Acid), GRAM (Glucosyltransferases-like GTPase Activators and Myotubularin), RCAR (Regulatory Components of ABA Receptors), PYL (PRY1-Like), and PRY1 (Pyrabactin Resistance1)

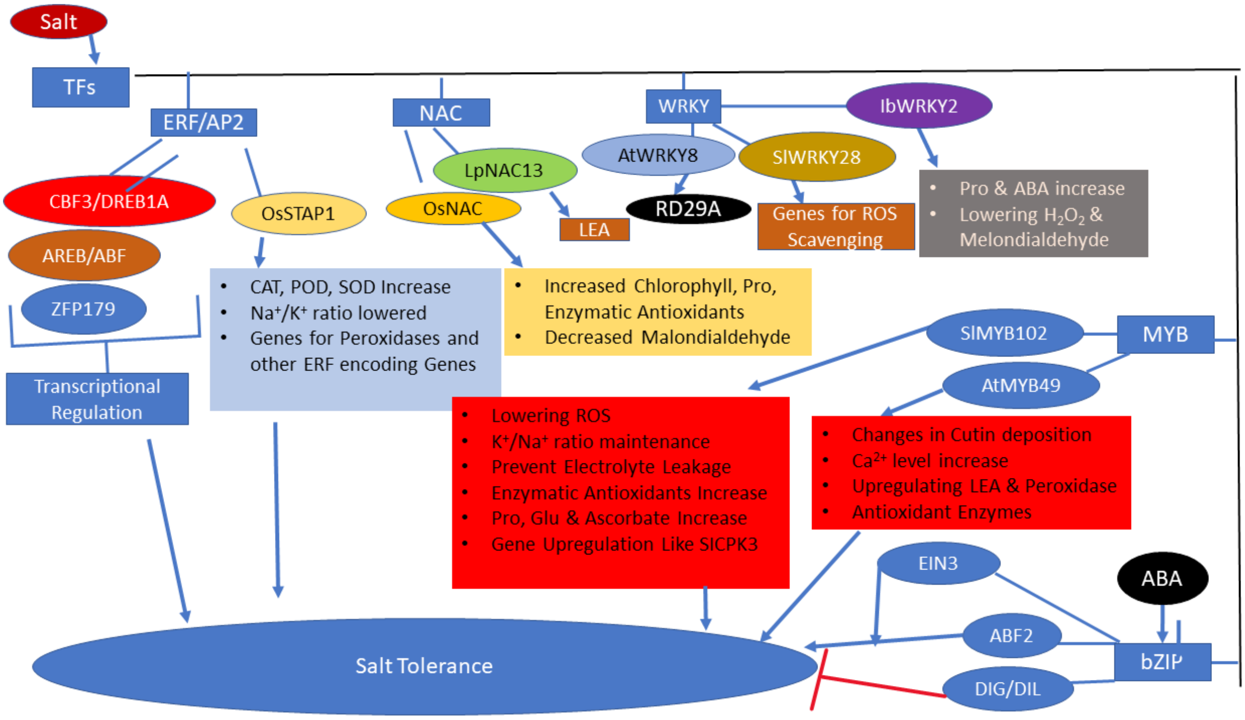


Figure 4: Role of Transcription Factors (TFs) in salt tolerance.

Many studies have described that salinity stress induces within genome DNA methylation and epigenetic variation, either natural or induced by mutations in DNA methylation mechanisms result from gene expression alteration mediating salt tolerance (Karan *et al.,* 2012; Wang *et al.,* 2014; Wang *et al.,* 2015; Huang *et al.,* 2013). A correlation between histone methylation alterations and inactivation or activation of genes induced by salt (Sun *et al.,* 2019); however, the role of epigenetic changes induced by salt stress in salt tolerance is yet to be arrived at fully.

CONCLUSIONS AND FUTURE PERSPECTIVE

Plant salt tolerance includes a cascade of responses at physiological, biochemical, and molecular levels. Comprehensive research viz; physiological, biochemical, and molecular studies have explained various salinity mechanisms regulating ion intake, exchange and balance, osmotic regulation, hormonal metabolism, antioxidant metabolism, and stress signaling. Besides, rapid expression of NtNHX1 increases plants salt tolerance by enhancing vacuolar Na^+ compartmentalization that declines the toxic accumulation of the ion in the cytoplasm that promotes growth in a saline environment. The determination of net Na^+ flux across the plasma membrane regulates the expression of SOS 1 (Na^+ efflux) and HKT1 (Na^+ influx). Environmental stress, particularly osmotic and ionic stresses, are liable for the decrement in yield, especially in arid and semi-arid regions. Production of ROS in different cell organelles chloroplast, mitochondria, and peroxisomes is due to prolonged environmental stresses. The normal functioning of the cell is disturbed by ROS as it attacks biomolecules like DNA, lipids, proteins, and carbohydrates. Under extreme stress conditions, ROS finally leads to cell death. For overcoming oxidative stress, plants have enzymatic and non – enzymatic antioxidants. Many workers have addressed various benefits of SOD, CAT, APX, GR, MDHAR, AsA in overcoming oxidative damage to the cell. There is an accumulation of osmolytes and osmoprotectants, such as proline and glycine betaine, to overcome salt stress's detrimental effects. These compounds help in osmotic adjustment and protecting subcellular structures. Salt tolerance of plants can be enhanced by increasing CO_2 concentration as it alleviates oxidative stress, which activates the oxidative system and increases the accumulation of compatible substances.

LEA proteins play a significant role in plant stress tolerance, but the elaborated mechanisms of plant stress protection remain undetermined. Under abiotic stress, distinct signaling pathways are regulated, including the MAPK cascade. MAPK molecules are a group of proteins that can negotiate various plant functions, like cell cycle, plant growth and development, plant response to stress. The integration of different MAPK pathways can be very beneficial for transgenic plant production, which is more resistant to salinity stress. Maintaining plant behaviour, particularly Na^+ cellular concentration under salt stress, is an important key issue to make plant salt tolerant. MAPK signaling can significantly affect such pathways by regulating proton pumps' activity, Na^+ localization into vacuoles, and regulating the cell cycle. There is a crosstalk between different signaling pathways during the stress and the interactions with phytohormones. At the molecular level-specific TFs, non-coding RNAs and epigenetic modifications play an essential role in countering salt stress and imparting salt tolerance.

The limitation of crop production due to salt stress and ensuring food security can be overcome by developing salt-tolerant crop plants by utilizing novel technologies like gene editing and resourceful genetic transformation. The prerequisite for these novel technologies is that candidate genes associated with salinity tolerance must be recognized and exploited. Though multiple studies are carried out, the are many areas of understanding salt-induced responses and plant adaptability which need more focus, including how a plant senses the salt stress at the cellular and whole plant level, what sort of changes occur at cellular levels like cell wall modifications, cell organelles response and signal integration, mechanisms of phytohormone involvement. The control of specific gene expression during salinity stress needs special attention to discover and understand the role of key players like TFs, non-coding RNAs, and epigenetic modifications.

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