REVIEW ARTICLE

Morphological and Molecular responses in plants to Salinity: An Overview

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Abstract

In the soils of arid and semiarid areas, salt stress is a serious threat which constitutes nearly 40% of the earth's land area. Salinity is the amount of dissolved mineral salts like the electrolytes of positive ions like Na^+, Ca^{2+}, Mg^{2+} and K^+ and negative ions like Cl^-, SO_4^{2-}, HCO_3^-, CO_3^{2-} and NO_3^- present in soil and ground. Salinity stress causes the generation of reactive oxygen species that limits the metabolism and destroys DNA, proteins, lipids and other macromolecules of the cell through oxidation. Under the influence of salinity, plants should fight against two main stresses: - (i) osmotic stress and (ii) ionic stress. In plants, balancing of ions is crucial due to high concentration of salt. Furthermore, the salt stress impacts on the inhibition of biochemical and physiological processes, whole plant growth through osmotic effects, particular ion toxicity, nutritional imbalances and disturbance in the hormonal homeostasis. To survive in saline environments, plants rely on a variety of stress-responsive proteins. These proteins include ion transporters that help maintain ionic balance. Proteins, dehydrins and proline biosynthetic enzymes support osmotic adjustment, while antioxidant enzymes protect against oxidative damage. Signal transduction proteins and transcription factors regulate stress-responsive genes, while aquaporins and heat shock proteins maintain water flow and protein stability. Traditional breeding methods have limited success in developing salt-tolerant crops due to the complex genetic basis of stress responses. In recent years, genome editing tools have emerged as a powerful alternative for precise genetic improvements in plants. Among these tools, the *CRISPR-Cas9* system has gained prominence due to its simplicity, accuracy and versatility.

Keywords: Salinity, Electrolytes, Reactive Oxygen Species (ROS), Ionic stress, Nutritional imbalances, Salt stress proteins.

Highlights:

- Salinity implies the presence of dissolved salts in soil, water having anions (Cl^-, SO_4^{2-}, HCO_3^-, CO_3^{2-} and NO_3^-) and cations (Na^+, Ca^{2+}, Mg^{2+} and K^+).
- Reactive oxygen species (ROS), which can be generated by excess ions, oxidatively damage proteins, lipids and DNA of the plants.
- Excessive salt interferes with hormone control, nutritional balance, biochemical and physiological functions.
- Ion balance is maintained by SOS pathway proteins and ion transporters.
- Stress-responsive genes are influenced by transcription factors and signal transduction proteins.
- Transcription factors and signal transduction proteins show direct effect on stress-responsive genes.
- Genetic engineering of salt tolerance by CRISPR-Cas9 technology, which holds promise for sustainable agriculture in saline environments.

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Introduction

There are many biotic and abiotic factors or stress, that alter the process of growth and development of plants, in which 'salinity' is one of the major 'abiotic factors' that causes the vital loss and retards the output mainly in regions like arid and semiarid (Vaidyanathan *et al*., 2003). The appearance of replaceable sodium ions in the root zone in that specific amount, which alters the healthy plant functioning, is known as 'salinity'. The 'salinity' is the amount of deteriorating rock salts like the negative and positive electrolytes, that are available in ground and soil water. The main positive ions in salt solution consist of ions of sodium, calcium, magnesium, potassium and the other main negative ions are chloride, sulphate, carbonate, bicarbonate and nitrate. Other compounds related to salinization in oversaline soils and water consist of molybdenum, barium, aluminium, silicon dioxide (Schmidhalter, 1993, 1999). Salts that are soluble in water gather in ragolith/soil to such an extent that affects the farming outcome, welfare in environmental and economic health (Rengasamy 2006).

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Apparently, around 40% and more agricultural land area will be soon come under the effect of salinization (Gilliham and Munns, 2015). Salt stress is the main trouble that impedes yield and overall development of plant and hinders the viable growth of contemporary farming. It has been found that about 1/3rd of the flooded area on earth are over-elaborated due to salinity and its main cause is the salts in upgrading columns of underwater and also low management of effluent and sprinkling techniques.

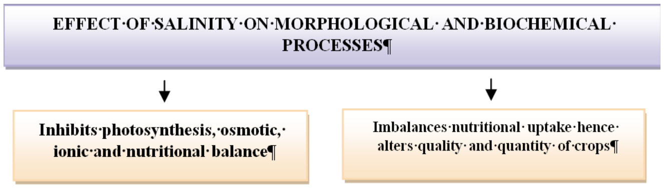

Fig. 1: Showing effects of salinity on morphological and biochemical processes

Extent of soil salinity in Uttar Pradesh and neighboring states

The latest estimates suggest that Uttar Pradesh has approximately 1.37 million hectares (Mha) of salt-affected land, primarily concentrated in districts like Etawah, Kanpur, Unnao, Raebareli and Hardoi (ICAR-CSSRI, 2024) (Table 1). Other neighbouring states also have substantial salt-affected areas.

Classification Of Salinity

According to Ghassemi *et al*., (1995), salinity may be classified into two types in which one is primary (1^o) salinity and second is secondary (2^o) salinity. The primary salinity comprises over the mixture of different salts from two different spontaneous mechanisms over the cross-period of time. The very first process is the disintegration of rocks bearing miscible salts as sodium chloride (NaCl), calcium (Ca) and magnesium (Mg) and also a certain minimal quantity of sulphates (SO_4^{--}) and carbonates (CO_3^{--}). The other process is the accumulation of salts related to oceans, including inlands by the association of rain and wind. The salinity construction of dissolved salt belongs to oceans and it is purely NaCl (Munns, 2005). In nature, the areas that are affected by salts are found broadly in saline, semi-saline areas as stated by Rengasamy *et al*., (2003).

It is quite acknowledged that salty water present in sub-soil is not related to the aquifer (Rengasamy, 2002). The mentioned specific type of salty water is known as 'transient salinity' as it may accelerate throughout soil-profiling, root zonal area, determined over the given period of time. The secondary salts occur through the reactions that alters the hydro-geological balance between rainfall and transpiration.

The prevalent causes are

- Replacement of annual vegetation and land clearing,
- Saline water or improper drainage.

Impact of salinity on the growth of plant or effects of salinity stress on plants

Salinity inhibits the biochemical processes, like photosynthesis, which affects the complete growth of the plant by the osmotic imbalance, nutritional imbalances, particular toxicity related to ions, or/and disturbed hormonal homeostasis. Salinity not only affects the morphology and physiology of plants but also imbalances the uptake of nutrients as shown in fig. 1, which alters the quantity and quality of crops. At the expense of some other nutrients: - salinity favours the uptake of some nutrients, owing to ionic imbalances.

An exogenous supply of salt ends up in the generation of byproducts that is *'reactive oxygen species'* (ROS), which destroy the building of cells (Dat and Van Breusegem, 2000). Salt stress is the crucial specification that hinders the yield of farm output, with inauspicious results on the impregnation of seeds, vitality of plants (Munns and Tester, 2008). Conclusively, salt stress reduces the carbohydrates, protein, oil percentage, polysaccharides, and total amino acid significantly. 'ROS' (Reactive oxygen species) impacts the disintegration of lipid-peroxidation which is present in the membrane, chlorophyll degradation, reducing membrane fluidity and selectivity (Verma and Mishra, 2005). The degradation in chlorophyll (Chl.) content; lipid-peroxidation which is measured by malondialdehyde (MDH) content, are found to be the 'marker' of *oxidative stress* (Del Rio *et al.,* 2000). There are various antioxidative enzymes like POx, SOD, CAT and APx that helps in detoxification of 'ROS' (Tuteja and Gill, 2010).

In salt stress, plants must raise a que of enzymatic e.g., Catalase (CAT), Glutathione Reductase (GR), Peroxidases (POx) and several non-enzymatic e.g., Ascorbate (ASC), Carotenoids (CAR), flavonoids, phenolics etc., activities. These are the various detoxification systems to protect against oxidative stress by scavenging these reactive oxygen species compounds to overcome damages caused by them in plants (Sairam and Tyagi, 2004).

Antioxidative proteins play a key role in plant 'defence mechanism' related to salt stress, by detoxifying superoxide and H_2O_2, has so far been reported (Jaleel *et al*., 2007; Esfandiari *et al*., 2011). Ascorbate (ASC) and Glutathione Reductase (GR) are 'antioxidants' helping in scavenging of H_2O_2 in combination with monodehydroascorbate (MDH) reductase and glutathione reductase (GR), which reforms ascorbate (Horemans *et al.,* 2000). There are several pigments like carotenoids, play key role in plants, as they show their direct role in the process of

Table 1: Extent of soil salinity in Uttar Pradesh and neighboring states (source: ICAR-CSSRI 2024)

State	*Saline Soils (ha)*	*Alkali Soils (ha)*	*Total Salt-Affected Area (ha)*
Uttar Pradesh	21,989	1,346,971	1,368,960
Haryana	49,157	183,399	232,556
Punjab	0	151,717	151,717
Rajasthan	195,571	179,371	374,942
Bihar	47,301	105,852	153,153
Madhya Pradesh	0	139,720	139,720
Uttarakhand	12,500	18,300	30,800
Total	326,518	2,125,330	2,451,848

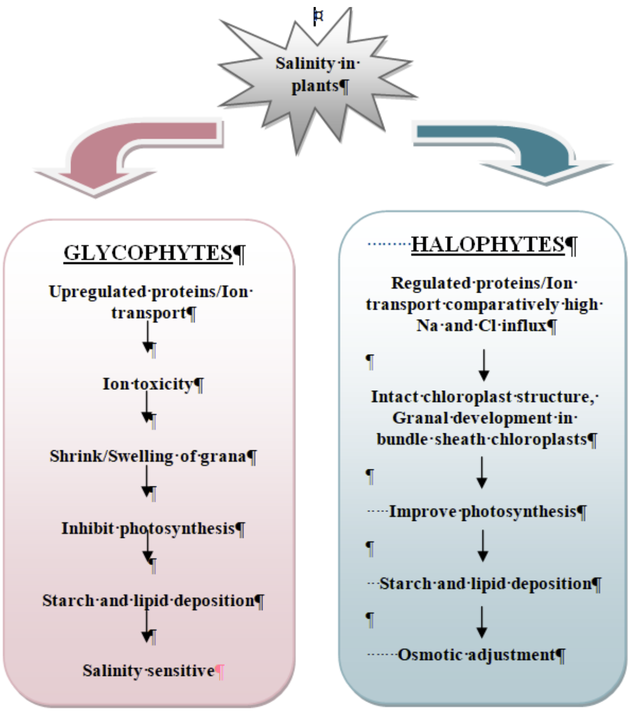

Fig. 2: Showing, how Lycophytes' and Halophytes plants adjust sensitivity and tolerance towards salt stress.

photosynthesis; their impact also found in oxidative damage management (Tuteja and Gill, 2010).

The phenolics show their presence in cell wall components and play an important role in the maintenance of developmental and growth processes, and also defence mechanisms of abiotic and biotic stress (Cheynier *et al*., 2013). *Reactive oxygen species* (ROS) regulate the metabolism of cells and cause damage through deterioration of deoxyribonucleic acids, lipids, enzymes/proteins, and other micro and macro molecules of the cell (Ahanger *et al*., 2020). The key supply of free oxygen (O_2^-) radicals in plant cells are plasma membranes, mitochondria, endoplasmic reticulum, chloroplasts and peroxisomes (Foyer and Noctor, 2009; Asada, 1999).

The plants show different tracks to detox the effects of reactive oxygen species (ROS) via a list of enzymes and proteins, either worthy solutes or non–enzymatic reactions and the antioxidants which are purely or in association to nullify diffusion damage (Ashraf and Foolad, 2007). For maintaining the salt-induced osmotic damage, the plants assemble suitable solutes comprising of proteins that are soluble, proline (PRO), soluble sugars and antioxidants such as ascorbate (AsA) reported by Munns-Bosch *et al*., (2005). The elements increase absorption of water by depletion of the diffusion potential of cytoplasmic content, as stated by Puniran-Hartley *et al.,* (2014).

Division of plants under salinity

Plants may be categorised in two main divisions on the basis of adaptation: the plants that can bear salt stress are named as 'halophytes' as *Rhizophora* L. and that cannot bear salt stress are called as 'glycophytes'. Many of the cereal crops, staple foods and vegetables are sensitive to salts even when the electrical conductivity is <4dSm^{-1}.

Adaptive operation of glycophytic crops under salinity

The salinity drops the production of crop which is contradictory to the increasing demand for food worldwide. High absorption of salt causes ionic imbalances and high osmotic-stress in the plants. Due to the outcomes of primary effects, the level of secondary stress like oxidative stress in plants also takes place. Many plants have developed counter pathways either to eliminate excess salts associated with the cells or/and to prevent their appearance inside all cells. The initial state and accumulation of salinity inside a plant, all main mechanisms like nitrogen fixation, photosynthesis, energy and lipid metabolism and were found severely affected (Parida and Das 2005; Baghel *et al*., 2016).

Under the influence of salt stress, plants need to tackle with two major stresses; ionic and osmotic. The osmotic stress instantly overcomes the effects of salinity around the roots, which causes water uptake inhibition, development of lateral bud and expansion in cells (Munn and Tester, 2008). On the other hand, imbalance in ions develops excess accumulation of sodium ions, particularly in leaves, which causes chlorosis and hence leaf mortality and necrosis and a drop in crucial cellular physiological pathways, including photosynthesis (Glenn *et al*., 1999), which imparts growth reduction and yield of farm output.

The major difference between plants that are salt sensitive and salt resistant are shown in fig. 2

As a result, to tackle with excess salt, the helpful planning for glycophytes is to maintain cytosolic sodium ionic levels lower at the cellular level; to maintain shoot sodium ions levels low throughout the plant parts. Abbasi *et al*., (2016) stated that in response to such elements, the equilibrium and maintenance of potassium ion show a remarkable change on the activity of salt-tolerance of plant. For, the salinity-bearing property of glycophytic plants, the equilibrium of raised cytosolic potassium and sodium ratios has been highly recommended to be important mainly in shoots (Hauser and Horie 2009). The assimilation of excessive salt in older leaves increases the chance of its degradation and hence lowers the uptake of growth regulators and carbohydrates to the meristematic tissues, and hence inhibits plant growth. Thus, the growth of plant is inhibited by a reduced rate of photosynthesis and also by uptake of excessive salt which influence the maintenance of particular metabolites that prohibited growth directly (Azza *et al*., 2007).

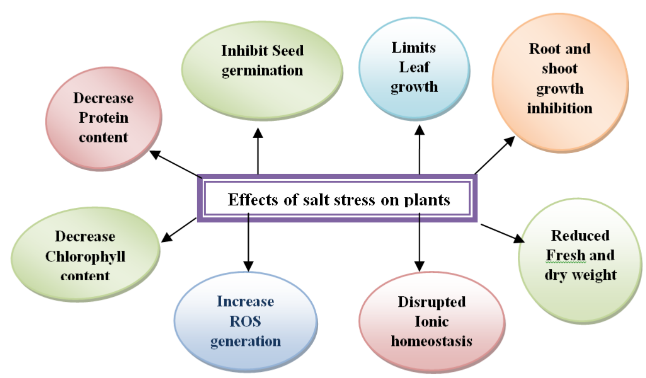

Fig. 3: Showing different effects on the plant which bears salt stress.

Effects on morphology of roots and leafy parts under salinity

Wu *et al*., (2016) reported that the performance of the root is determined on the basis of internal structure of the roots like its length, root diameter, etc., the making ability of plants which access water and nutrients and the increment in the rate of transpiration in plants. Hence, root system acts as an edge between plants and solum, so appropriate roots can assist the growth of the shoot and improvement in plant output (Vamerali *et al*., 2003). Acosta-Motos *et al*., (2017) stated that the multiple systems of roots reflected to be good for plant growth and in return how plant responses under salt stress on plant, as shown in fig. 3. According to Steudle 2000; Ranathunge *et al*., (2010), the accessibility of water to roots also specifies another root features, like the diameter, number of vessels in xylem, broadening the cortex of root, aggregation of root-hairs in exodermis and suberin accumulation in endodermis of root.

Shannon *et al*., (1994), reported that the abiotic elements inside soil like change in temperature, lack of oxygen, high level of salt and mechanical blockage may also show remarkable effects on anatomy of root. The epidermis of root under high salt levels is often irregular convoluted and thickened. Batanouny *et al*., 2001, stated that in the roots of solid woody plants, salinization creates the suberised hypodermis and endodermis and consequently makes a structure called 'casparian strip' near the apex of root, is totally independent of that occur in non-salty roots.

As a matter of fact, a decrease in leaf growth is very first response of glycophytic plants when an exogenous supply of high salinity (Termaat and Munns, 1986). Ruiz-Sanchez *et al*., 2000, suggested that the reduced area of the canopy may be considered as an avoidance response that lowers the rate of transpiration under the influence of stomatal closure. Colmer *et al*., 2006, reported that the attainment can induce ion toxicity inside the roots, which limits the assembly of such toxic ions into outer portion of plant.

Rodriguez *et al*., 2005, showed that due to the impact of salinization, the properties of cell wall and leaf turgor change with a decrease in rate of photosynthesis, resulting in a reduced total leaf blade area index. Rate of high concentration of salt usually lowers the rate of growth of stem also and a decrease in area of the leaf-blade and the stem broadening of the stem results outcomes in depletion of aerial parts. Hsiao and Xu (2000), mentioned that the increase and decrease in root compared to shoot very first response to salinity, related with water scarcity or lodging (osmotic effect) in comparison to a particular salt output. A prominent root segment under salinity can assist in retaining of toxic-ions concentration in respective parts; manage their transport to aerial-associated parts.

This retaliation can create a distinctive pathway of plants towards aversion/survival under salinity, as reported by Cassaniti *et al*., 2009, 2012. According to Munns and Tester, (2008), high concentrations of salt in the supplied water result in a reduction in plant growth, restricting the leaf enlargement (Cramer, 2002) and altering the bond between roots and shoots reported by Tattini *et al.,* (1995). The Zekri and Parsons (2017), stated that due to the influence of salt-stress, few species of plant have reflected an increased biomass of dry root than biomass of dry shoot, showing an increase in root: shoot ratio that is supposed to enhance the source or sink ratio for the water: nutrients ratio during the same state.

Anatomy of leaf and changes in its ultrastructure under salinity

Longstreth and Nobel (1979), noted that salt stress creates an increment in the diameter of epidermis and mesophyll, increase in diameter and length of palisade cell, broadening in the cells of palisade and spongy cell in leaf-blade of *bean* and *Atriplex*. Contrarily, both epidermal as well as mesophyll diameters and inter-cellular spaces reduced prominently in sodium-chloride (NaCl) imposed leaf of mangrove *Bruguiera parviflora* L. (Parida *et al*., 2004). In leaves, spaces between the cells were also reduced under salt-stress (Delfine *et al*., 1998).

According to Mitsuya *et al*., (2000), salinity imparts: (1) formation of large vacuole and fragmented protuberances of endoplasmic reticulum, (2) lowers the number of cristae of mitochondria and enlargement of mitochondria (bioblast), (3) fragmentation and vesiculation of tonoplast (4) cytoplasmic abasement through the help of mixture of vacuolar matrix and cytoplasm in leaf-blades of sweet potato. In the shoot of potato plant, salt stress forms skirt of cells, reduces the space between cells and reduced number of chloroplasts as stated by Hameed *et al.,* (2021). Salinity creates reduction in plant's leaf-blade area index and stomatal-density in the plant tomato (*Lycopersicon*) under salinity (Romero-Aranda *et al*., 2001).

Physiological adaptations of plants under salinity

There are many physiochemical processes that are influenced by abiotic factors and they arbitrate the reaction of flora towards salt stress. The production of organic matter is a measurement of total rate of photosynthesis, hence abiotic stress influences growth which is also found to affect the process of sunlight into biochemical energy. Parida and Das (2005), reported that the effects of salinization in both long and short term. In short term, salt stress inhibits the pursuit of photosynthesis by stomatal impediment, leading to a decrease in carbon assimilation. Hernandez and Almansa, (2002), stated that this results in rapid growth ceasing, just after a few hours of exogenous supply of salt.

In case of long term, salinity also alters the rate of photosynthesis due to the association of high salt in apical leaves and a decrease in concentrations of carotenoids and chlorophyll in glycophytic plants as mentioned by Stepien and Johnson 2009; Duarte *et al*., 2013; Baghel *et al*., (2016).

Due to the closure of stomata, the rate of photosynthesis decreases as there is disturbance in the electron chain of photosynthesis and also the inhibition or breakage of enzymes of Calvin cycle, as PEPcase, (RuBisCo) ribulose-5-phosphate carboxygenase, ribulose-5-phosphate kinase, glyceraldehyde-3-phosphate dehydrogenase or fructose-1,6-bisphosphate, as mentioned by Parida and Das (2005), Meloni *et al*., (2008). Ashraf, (2013), reported that under the saline effects, it is well known that salt-tolerance activity of plants reflects unchanged or an increase in chlorophyll concentration, on the other side levels of chlorophyll drop in species of salt-sensitive plants, hence proving that this marker may be regarded as a biochemical tag of salt-tolerating efficiency in the plants.

Impact of Salinization on Nitrogen Fixation

Salinization reduces the extent of 'nitrate reductase activity' (NRA) in foliose of several plants reported by Baki *et al*., (2000). The main reason of the reduction in the levels of NRA is associated with the appearance of Cl^-ions in the external tissues in the leaf-blade. Flores *et al*., (2000), stated that the sequence of chloride ions is shown due to depletion in the levels of NO_3^- uptake and hence resulted in the low concentration of NO_3^- in leaves, although there is an immediate outcome of Cl^- on the enzymatic activities which cannot be ignored. Under NaCl stress, the level of concentration of nitrate decreases in blades, but on the other hand increases in radicle, and level of NRA decreases in blades of plant under the influence of high salt in *Zea mays* L., as stated by Baki *et al.,* (2000).

Soussi *et al*., (1998), showed that the activity of nitrogenase and the fixation of nitrogen by diminishing the nodulation inhibition under salinity in chickpea (*Cicer arietinum* L.). Extreme level of salinization gets deplete the concentration of leghaemoglobin and also the activity of nitrogenase in root lumps of soybean (Comba *et al*., 1998). The manifestation of NaCl on root nodules of legumes such as alfalfa, common bean and soyabean shows a reaction in heavy drop in plant growth linked with momentary reduction of nitrogenase activity and growth of nodules. The salinization interferes with the concentration of nitrate and management of enzyme nitrate reductase activity (NRA) in blades of *Zea mays* L. By short-term exposure of salt, the activity of acetylene reduction drops down in common bean and hence measured the nitrogenase activity (Serraj *et al.,* 2001).

Generally, salinization influences the level of glutathione and ascorbate much in salt-sensitive plants in comparison to tolerant plants. In the genotype of sodium chloride sensitive towards pea plants, after 15 days of salt stress exposure sodium chloride stress generated a 50% reduction in total ascorbate (ASC), that may be ascribed to a decrease of both DHA (oxidised) and ASC (reduced) types. In genotype of sodium chloride tolerant, salinity decreases the level of ASC and DHA but its level decreases in sensitive plants (Hernandez and Almansa 2002). According to Lee *et al*., in (2013), the level of 100mM NaCl stress declines the content of ASC in leaves of rice cultivar IR-29 which is salt sensitive, but there is ineffective record in blades and radicle of salt-tolerant rice cultivar.

The sustentation of phytohormones under salinity

The biochemicals like auxin, cytokinins and gibberellins which are associated with the regulation and development of plants; and ethylene and abscisic acid are growth reducers. During the course of salinity, changes in levels of ABA and ethylene are observed. For example, upon exposure of salt in White Lupin (*Lupinus albus* L.), in response to abscisic acid initially stomata are closed and afterwards abscisic acid formation takes place and is transported to the leaves, as mentioned by Chen *et al.,* (2020), stated that the raised level of abscisic acid concentration in leaf-blade and rest of the tissues are not only influences stomatal movements but also ameliorates the salt accumulation by diffusion management.

Kukreja *et al*., (2005), stated that due to the influence of the high salt-treated *Chickpea* and *Faba bean*, the formation of ethylene takes place and the related forerunner 1-aminocyclopropane-1-carboxylic acid (ACC) in radicle and *nodules* activates fatuity of leaves. Hence, the levels of salinity change the level of hormones that are released under the salinization, which induces the change in photosynthesis, plant growth and osmotic adjustment.

Proteins involved in salt stress plants

Salt stress in plants triggers complex physiological and molecular responses that involve a broad spectrum of stress-responsive proteins. These proteins enable plants to maintain ionic balance, protect cellular structures, and ensure proper metabolic function under salinity stress. The article by Sahu *et al*., (2022) comprehensively reviews these protein classes and their roles.

Ion Transport and Homeostasis Proteins

- HKT (High-Affinity K^+ Transporters) **–** Help to prevent Na^+ accumulation in shoots by retrieving it in roots **(**Munns and Tester, 2008).
- NHX (Na^+/H^+ Exchangers) - Facilitate vacuolar sequestration of Na^+ to avoid cytotoxicity (Apse *et al*., 1999).
- SOS Pathway Proteins
- SOS1 (Na^+/H^+ antiporter): Effluxes Na^+ at the plasma membrane.
- SOS2 (CIPK24 kinase) and SOS3 (CBL4 Ca^{2+} sensor): Activate SOS1 in response to salt-induced Ca^{2+} signals (Zhu, 2001).

Osmoprotectant-Related Proteins-

- LEA (Late Embryogenesis Abundant) Proteins – Stabilize membranes and proteins during water deficit (Tunnacliffe and Wise, 2007).
- Dehydrins - Specialized LEA proteins that are hydrophilic and protect cellular structures (Close, 1997).
- P5CS (Pyrroline-5-carboxylate synthetase) - Catalyzes proline biosynthesis, enhancing osmotic adjustment (Szabados & Savoure, 2010).

Antioxidant Defense Proteins

- SOD (Superoxide Dismutase) - Converts superoxide radicals into hydrogen peroxide (Alscher *et al*., 2002).
- CAT (Catalase) and APX (Ascorbate Peroxidase) - Further detoxify hydrogen peroxide to protect cellular components (Mittler, 2002).
- Glutathione-S-Transferases (GSTs) - Conjugate glutathione with ROS byproducts for detoxification (Dixon *et al*., 2002).

Heat Shock Proteins (HSPs)

HSP70, HSP90, sHSPs (Small HSPs) - Act as molecular chaperones, refolding denatured proteins under stress.

Signal Transduction Proteins

- CDPKs (Calcium-Dependent Protein Kinases)- Perceive calcium signals triggered by salt stress and initiate phosphorylation cascades (Cheng *et al*., 2002).
- MAPKs (Mitogen-Activated Protein Kinases)- Mediate stress-responsive gene activation (Nakagami *et al*., 2005).
- SnRKs (Sucrose Non-Fermenting1-Related Protein Kinases)- Link energy signaling with stress responses (Halford & Hey, 2009).

Transcriptional Regulators

- DREB (Dehydration-Responsive Element Binding proteins)- Bind to DRE/CRT elements in promoters of stress-inducible genes (Nakashima *et al*., 2009).
- bZIP, NAC, MYB and WRKY Transcription Factors- Modulate diverse gene networks during abiotic stress (Yamaguchi-Shinozaki and Shinozaki, 2006).

Aquaporins

PIPs (Plasma Membrane Intrinsic Proteins)- Regulate water flux and maintain cellular water status under salt stress (Maurel et al., 2008).

Ubiquitin-Proteasome System Proteins

E3 Ligases and Proteasomal Subunits- Control selective degradation of misfolded or damaged proteins, maintaining proteostasis (Stone, 2014).

Salt stress-responsive proteins play pivotal roles in plant adaptation to high salinity. From membrane-bound transporters to antioxidant enzymes, transcription factors and protein kinases, each class contributes to a coordinated stress defense system. The integration of proteomic and genetic tools, as emphasized by Sahu *et al*., (2022), holds promise for enhancing salt tolerance in crops through targeted biotechnological approaches.

CRISPR-Cas for Enhancing Salt Stress Tolerance in Plants

One significant abiotic stressor that significantly impairs plant development and agricultural output globally is salinity. Crop yields are eventually decreased by salt stress because it causes ion imbalance, osmotic stress and oxidative damage in plants. By precisely manipulating stress-responsive genes, recent developments in genome editing, especially the CRISPR-Cas system, have created new opportunities for enhancing crops's resistance to salt stress.

Role of CRISPR-Cas in Salt Stress Tolerance

Editing important transcription factors and regulatory genes involved in salt stress responses has been accomplished with success using the CRISPR-Cas9 technology. Researchers have been able to improve tolerance mechanisms by targeted mutagenesis or gene knockouts, which improve antioxidant enzyme activity, ion homeostasis and osmolyte accumulation.

Several key examples of CRISPR-Cas in Salt Stress Tolerance

Knockout of OsRR22 in rice

To create salt-tolerant rice lines, CRISPR-Cas9 was used to modify OsRR22, a type-B response regulator involved in cytokinin signaling. When compared to wild-type plants, the modified plants displayed better shoot and root development in salty environments (Zhang *et al*., 2019).

Editing of AtHKT1; 1 in Arabidopsis

A sodium transporter is encoded by the AtHKT1;1 gene. Better sodium exclusion and increased salt tolerance were the outcomes of its overexpression or CRISPR alteration (Wang *et al*., 2018).

Modulation of transcription factors such as NAC and DREB

Genes like OsNAC2 and OsDREB2A, important transcription factors controlling stress-responsive genes, have been altered with CRISPR-Cas. By enhancing the synthesis of osmoprotectants, knock-in and activation techniques have demonstrated enhanced tolerance to salt (Mao *et al*., 2021).

CRISPRa (CRISPR activation) techniques

Cutting-edge methods such as CRISPRa provide a safer and perhaps non-GMO method of managing stress by activating endogenous stress tolerance genes without changing the DNA (Lowder *et al*., 2015).

Future applications of CRISPR-Cas systems are developing quickly, and when more stress-related genes and regulatory networks are found, it is anticipated that their usage in salt stress tolerance will grow. The creation of base editing and CRISPR multiplexing technologies might hasten the production of crops resistant to salt.

Conclusion

Overall, salinity affects plant development by upsetting physiological processes; as a result, an ion imbalance leads to oxidative damage. The "root: shoot" ratio rises in salt-sensitive plants because salinity primarily damages the root zone that comes into contact with excessive salt. As the amount of ethylene and abscisic acid increases, the effects of salinity also affect hormonal homeostasis. However, plants have a number of defense mechanisms, such as storing salt in vacuoles to help them withstand high salt levels and enable them to thrive in unfavorable conditions. By preserving ion balance and lowering oxidative stress, salt stress-related proteins help plants withstand salinity. While antioxidant enzymes scavenge dangerous reactive oxygen species, transporters control the amounts of Na and K. Dehydrins and LEA proteins regulate stress-inducible genes and safeguard transcription factors and cellular structures. A revolutionary method of addressing salt stress is the use of CRISPR-Cas9 technology in plant genome editing. Stress-resilient crop types have been developed more quickly thanks to CRISPR, which has enabled targeted genes linked to salt tolerance. The potential of this technique to enhance characteristics including ion transport, osmotic balance, and stress signal transduction is demonstrated by successful case studies in rice, *Arabidopsis* L. and other crops. Incorporating CRISPR-Cas into crop development tactics offers significant potential for sustainable agriculture and global food security as we confront growing environmental problems. To reach its full potential in the sector, further research, clear regulations and public approval are essential.

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Author's Contribution

The corresponding author is experienced in the branch of plant nutrition and stress physiology of plants since last 18 years. Afreen Naaz, Swati Singh, are currently following their Ph.D. under the supervision of the corresponding author in the Department of Botany, University of Lucknow, Lucknow. Dr Rahul Verma has been awarded a Doctorate and is presently working in a Centre of Excellence project scheme under the supervision of the corresponding author. All the authors have keen interest in research area in the branch of Plant nutrition and plant stress physiology.

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