REVIEW ARTICLE Agricultural Reviews, Volume 45 Issue 2: 185-195 (June 2024)

Insights into the Detrimental Impacts and Coping Mechanisms under Salinity Stress in Mungbean (*Vigna radiata* L.)

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10.18805/ag.R-2628

ABSTRACT

Global food production is seriously threatened by salinity stress, which is becoming more severe due to human activity. For the majority of people worldwide, mungbean is a significant pulse crop and a rich source of protein and calories and hence is rightly marked as “Poor man’s meat” and “rich man’s vegetables”. Salt stress, on the other hand, negatively affects the productivity of the mungbean since it causes decreased germination, reduced growth and development, interrupted photosynthesis, hormonal imbalance and eventually decreased yields. Consequently, developing mitigation strategies to deal with salt stress requires a greater understanding of how plants respond to salinity stress. The present review highlights the detrimental effects of salt stress and the physiological and biochemical tolerance mechanisms in mungbean.

Key words: Mungbean, Oxidative stress, Salt stress, Tolerance mechanism.

Abiotic stresses are thought to be the cause of a huge decrease in crop output, posing a significant risk to global food security. Soil salinization is a major abiotic stress that hinders plant growth and crop production worldwide (Ahmad *et al*., 2019; Daliakopoulos *et al*., 2016). Soil salinization has occurred in approximately 20% of irrigated land which accounts for one-third of land for food production (Shrivastava *et al*., 2015). Arid and semi-arid regions are particularly susceptible to soil salinization (Fahad *et al*., 2015), where rainfall is insufficient for growing food crops and irrigation is employed to promote crop yield. This problem will worsen due to continued global warming and extreme climate fluctuations which disturb the water cycle (Ullah *et al*., 2021). However, to feed a population that is still expanding and to fulfill the first sustainable development goal of the United Nations, a world free from hunger, agricultural production must rise by 70% by 2050 (El-Sabagh *et al*., 2021).

Mungbean is an important pulse crop native to India belonging to the family Fabaceae. The world’s mungbean growing area is approximately 7.3 million ha and the production is approximately 5.3 million tones with India and Myanmar each supplying about 30% of this, China 16% and Indonesia 5% (Nair *et al*., 2022). China is the largest exporter (Misiak *et al*., 2017) and India is the largest importer of mungbean (Mohan *et al*., 2020).

The short life span and nitrogen-fixing ability in the soil make mungbean an important crop in most cropping systems (Hanumantha Rao *et al*., 2016; Somta and Srinives, 2007). The symbiotic relationship between *Rhizobium* and mungbean allows it to fix atmospheric nitrogen 58-109 kg per ha mungbean. It can give the soil a lot of nitrogen (30 to 251 kg/ha) and biomass (7.16 t biomass/ha) (Sengupta, 2018). The ability to fix nitrogen not only allows it to meet its own nitrogen needs but also supports succeeding crops. It can be utilized as a cover crop either before or after cereal crops (Le *et al*., 2021). Although mungbean is evolved to tropical and subtropical lowlands and is comparatively resilient to abiotic stresses like heat and drought, mungbean is more negatively impacted by soil salinity than other crops. The effects of salt stress on plants and symbiotic bacteria, such as *Rhizobium sp*., which are necessary for biological nitrogen fixation (BNF), include growth retardation and decreased yields (Kumar *et al*., 2020). A plant under salinity stress due to ion toxicity and nutritional imbalance undergoes several morphological, physiological and biochemical changes, which obstruct its growth and development (Plaut *et al*., 2013). Salinity stress reduces mungbean yield by more than 60% even at 50 mM sodium chloride (Desai *et al*., 2022). Salinity negatively affects germination, vegetative growth and reproductive development, especially flowering and pod-filling stages and ultimately the yield (Sehrawat *et al*., 2015).

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How to cite this article: Sinky, Sarita, Sapna, Soni, A., Ahlawat, P. and Sharma, K.D. (2024). Insights into the Detrimental Impacts and Coping Mechanisms under Salinity Stress in Mungbean (*Vigna radiata* L.). Agricultural Reviews. 45(2): 185-195. doi: 10.18805/ag.R-2628.

Submitted: 25-02-2023 **Accepted:** 16-05-2023 **Online:** 12-06-2023

Mechanism of salt stress on mungbean

There are two main ways in which high salinity affects plants: first, high salt concentrations interfere with the ability of roots

to draw water from the soil and second, high salt concentrations within the plant them selves can be toxic. A two-phase model describing the osmotic and ionic effects of salt stress was proposed by Munns *et al*. (1995) (Fig 1).

Osmotic effect

In salinity stress environments, soluble salts decrease the water potential and make water unavailable to plants hence creating a situation of physiological drought.

Specific ion effect

Ion-specific toxicity, generally, is because of certain ions like sodium, chloride and sulphate which are taken up in larger quantities than normal. Most plants especially crops are highly susceptible to this stress (Carillo *et al*., 2011).

Effects of salinity stress

Effects of salinity stress on growth parameters

Salinity stress influences the growth characteristics of mungbean through osmotic and ion toxicity, including germination, seedling growth and survival, vegetative growth (plant height, number of leaves, leaf area, membrane thickness and number of secondary branches and nodule formation) (Sehrawat *et al*., 2019; Acosta-Motos *et al*., 2017). In mungbean, the total number and dry weight of nodules per plant was reduced under saline conditions (Amir *et al*., 2013). Salinity also reduced nodule formation, dry weight of nodules, nitrogen fixation and root hair formation which may be detrimental to the crop in stressed conditions (Sehrawat *et al*., 2015). The increase in the root-to-shoot ratio is a typical response to salinity stress (Patiwi *et al*., 2021). Root dry weight and shoot dry weight are also negatively affected by salinity stress. The final vegetative phase and pod filling are more susceptible to salinity stress than the early vegetative phase (Subashree *et al*., 2021). A reduction in fresh weight and dry weight of the roots of mungbean was observed in the plants under salt stress when compared with the control (Farheen *et al*., 2018) (Fig 2).

Effect of salinity stress on photosynthesis

High concentrations of Na^+ and Cl^- are toxic in the cell, negatively affecting the photosynthetic capacity (Khan *et al*., 2019). Salinity reduced the net photosynthesis, stomatal conductance and intercellular CO_2 concentration by 23-30% compared to control plants of mungbean (Khan *et al*., 2014; Hernandez *et al*., 1999). The inhibition of the photosynthetic capacity under salinity might be due to the closure of the stomata, which reduces the availability of internal CO_2 (Zulfiqar *et al*., 2022). Salt stress can also reduce photosynthetic activity by affecting the non-stomatal

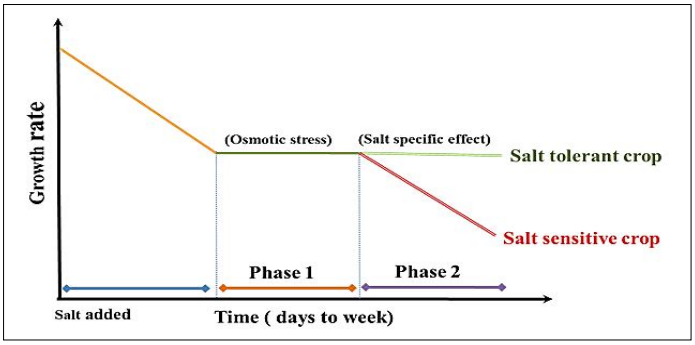


Fig 1: Schematic representation of two-phase growth response to salinity, adapted from Munns (1995).

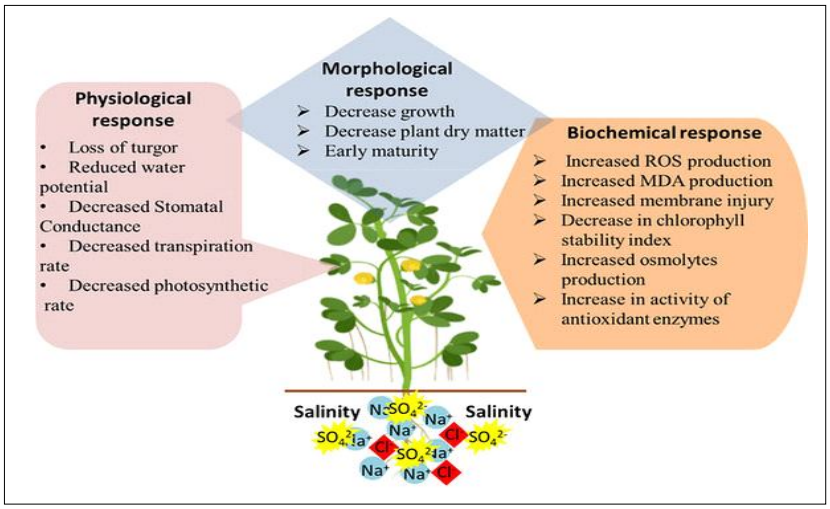


Fig 2: Changes in physiology and biochemistry of plant under salinity stress.

attributes such as the destruction of green pigments, lowering the leaf area, or by decreasing the activity of photosynthetic enzymes in the Calvin cycle (Nawaz *et al*., 2010). As a result, there is a lower contribution of carbohydrates to young leaves, with a reduction in the growth rate of shoots. Plant growth has directly linked with photosynthesis, transpiration, stomatal regulation and ionic absorption. Accumulation of toxic ions under salinity stress reduced the water and osmotic potential which further caused disturbances in photosynthetic processes (Chaves *et al*., 2009). The internal reduction of CO_2 during stomatal closure lowers the activity of various enzymes, notably RuBisCo which restricts carboxylation and lowers the net photosynthetic rate (Long *et al*., 2006). In an experiment by Khan *et al*. (2010) the activity of carbonic anhydrase, photosynthesis, stomatal conductance, intercellular CO_2 concentration, transpiration rate and water use efficiency was reduced by 36.4%, 18.2%, 9.7%, 10.8%, 15.8% and 20.5%, respectively, owing to 50 mM NaCl, compared to the control in mungbean cultivar. Salinity caused a reduction in chlorophyll and carotenoid contents which in turn resulted in pronounced chlorosis and necrosis in leaves. Leaf chlorophyll content decreased with increasing salt levels in mungbean (Farheen *et al*., 2018). A decrease in photosynthetic pigments reduced the photosynthetic efficiency of the plants in mungbean plants (Sehrawat *et al*., 2015). Photosynthesis is the primary determinant of crop yield and the efficiency by which a crop captures light and converts it into biomass over the growing season is a key determinant of final yield, be that biomass or grain (Simkin *et al*., 2019).

Effect of salinity stress on plant water relations

Plant-water relations explain the behavior of plants in terms of how they control the hydration of their cells, which has important implications in the physiological and metabolic processes that determine the quantity and quality of plant growth (Mahmood *et al*., 2016). Salinity disturbs a plant's water relations due to decreased availability of water from the soil solution as a result of lowered osmotic potential triggered by the toxic effects of the sodium and chloride ions (Munns *et al*., 1995). Early responses to water and salt stress are very similar because salts hinder the absorption of water through the root system due to the osmotic effect. In an experiment by Subashree *et al*. (2021) 100 mM NaCl on mungbean showed 0.46 fold decrease in the relative water content levels compared to the control set, whereas the plants exposed to 300 mM NaCl showed a drastic decrease of RWC *i.e*., 3.27 folds compared to the control. Similarly in an investigation by Mahmood *et al*. (2016) salt stress induced a noticeable decrease in RWC, with the lowest RWC noted for the 7.81 dSm^{-1} salinity treatment in mungbean plants. This indicates that with growing levels of NaCl there is a decline in the RWC levels. In an investigation by Khan *et al*. (2010) water use efficiency was decreased by 20.5% at 50 mM NaCl, compared to the control in the mungbean cultivar. Due to the accumulation of ions mainly Na^+ ions inside the cell which disturb the osmotic balance in the cell, so, absorption and translocation of water get reduced in salinity, as observed by Ali *et al*. (2012) in an experiment on mungbean.

Effect of salinity stress on mineral uptake

An excess of Na^+ and Cl^- ions in plants hinders the uptake of essential nutrients from the soil, which alters the plant processes. A reduction in K^+, Ca^{2+} and Zn^{2+} uptake and an increase in Na^+ and Cl^- uptake was observed, which inhibit the absorption of K^+, NO^-, PO_4^{-3} and many other essential nutrients (Lotfi *et al*., 2020). In an experiment conducted by Khan *et al*. (2010) mungbean plants grown with 50 mM NaCl exhibited an increase of 17.4% and 30.1% in Na^+ and Cl^- content and a decrease of 20.8%, 23.3%, 19.3% and 18.2% in N, P, K and Ca content, respectively, compared to the plants grown under non-saline conditions. Similar results were observed by Lotfi *et al*. (2020) in an experiment conducted on mungbean under salinity stress. Root and shoot Ca content decreased by 63% and 71%, respectively; Mg content by 24 and 39%, respectively and Zn content by 48% and 21%, respectively in salt-affected mungbean seedlings when compared to control seedlings in an experiment by Nahar *et al.* (2016).

Salinity-induced oxidative damage

Oxidative stress implies the "imbalance between oxidants and antioxidants in favor of the oxidants, leading to a disruption of redox signaling and control and/or molecular damage" (Hasanuzzaman *et al*., 2020; Sies, 2018). Salinity-induced osmotic stress, ionic stress and other factors in the total lead to the overproduction of ROS, over generation of ROS disrupt the equilibrium between ROS accumulation and scavenging, ultimately, resulting in oxidative damage to cell organelles and membrane components, protein oxidation, lipid peroxidation, enzyme inactivation, chlorophyll degradation and destruction of nucleic acids under stressful conditions (Hasanuzzaman *et al*., 2021). For example, salinity stress causes stomatal closure and hinders carbon dioxide (CO_2) entrance into leaves. This restrains CO_2 fixation and enables the chloroplast to stimulate immense levels of energy, which further develops the reactive oxygen species (ROS). The most important ROS are hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet-}$), singlet oxygen ($^1O_2$) and the hydroxyl radical ($^{\bullet}OH$) (Bhattacharjee *et al*., 2019; Khan *et al*., 2010) (Fig 3). The content of H_2O_2, TBARS and electrolyte leakage increased several fold under NaCl in comparison to the control in an experiment conducted by in mungbean. Similar results were obtained by Mankar *et al*. (2021), increased salt concentrations elevated the MDA content in mungbean. Membrane damage increased with increasing salt concentration from 75-125 mM NaCl and Khan *et al*. (2010) observed similar results in the content of H_2O_2 and TBARS and electrolyte leakage increased several-fold under NaCl in comparison to the control.

Mechanisms of salinity stress tolerance in mungbean

Mungbean, like other plants produce multiple alterations in physiological traits, metabolic pathways and molecular networks to perform preeminent under salinity stress. The mechanisms of salt tolerance in mungbean are complex as the plant produces numerous alterations in hormonal balance, antioxidant defense mechanism, osmotic regulation and ion exclusion (Fig 4).

Osmoregulation and osmoprotection

Mungbean uses the well-known approach of osmoregulation, like many other crop plants, to lessen the negative impacts of osmotic stress in salinity stress conditions (Chauhan *et al*., 2022). Mungbean plants accumulate various organic compounds (Table 1), which helps to reduce osmotic stress. Osmoregulation is responsible to prompt the defense mechanism against osmotic stress for regulating the plant-water relationship. The osmoprotectants are generally hydrophilic, with low molecular weight and without any net charge hence don't disturb normal metabolic reactions (Zulfiqar *et al*., 2020; Slama *et al*., 2015; Saha *et al*., 2010). In Mungbean plants, the salt-tolerant cultivars had high proline and amino acids with minimum protein contents as compared to the salt-sensitive varieties. Various concentrations of organic and inorganic solutes result in osmotic adjustment which varies with species and cultivars. In an experiment conducted by Subashree *et al*. (2021) with an increase in salinity a significant enhancement (2.69 fold increase) in proline activity and a 4.6 times increase in the leaf total soluble sugar content over control conditions in mungbean plants.

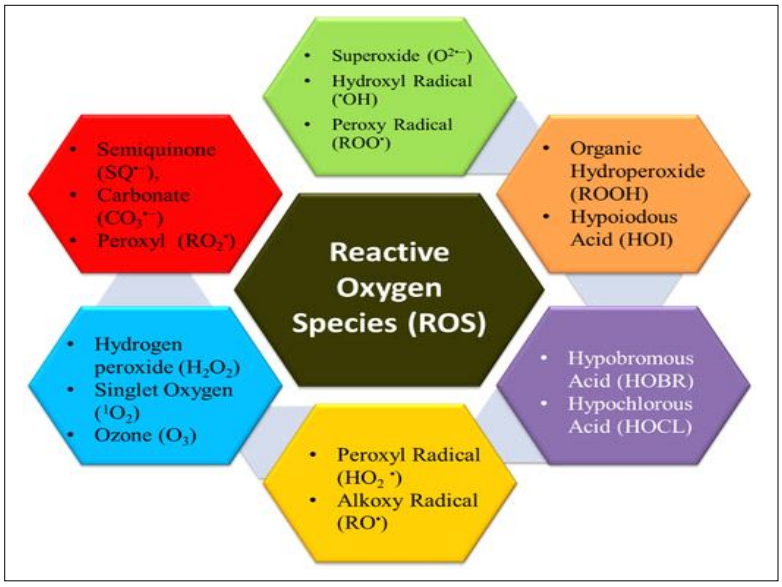


Fig 3: Types of reactive oxygen species (ROS) in plant cell.

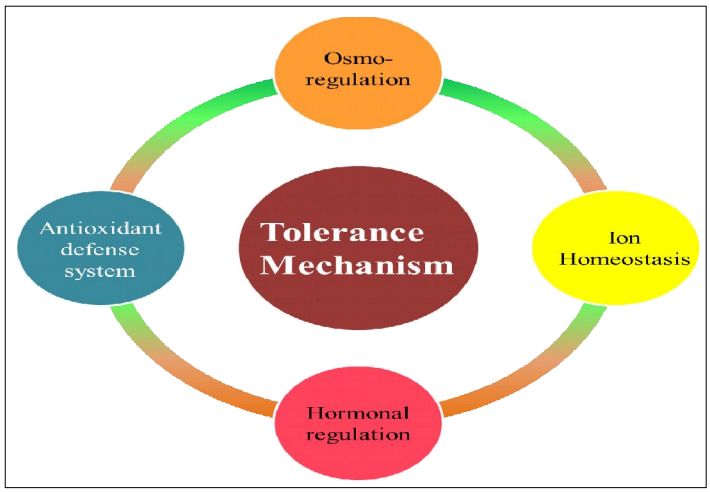


Fig 4: Tolerance Mechanism of plants against salinity stress.

In an investigation by Saha *et al*. (2010) NaCl pretreatment significantly increased the proline content in roots and leaves of the mungbean plants *i.e*. 0, 40% and 160% respectively in roots and by about 8%, 60% and 312% in leaves under 50, 100 and 150 mM NaCl treatments.

Ion homeostasis

Regulating intracellular Na^+ and K^+ ions concentration is fundamental for the various enzyme's performance in the cytosol, maintaining the membrane potential as well as cell volume (Shabala and Pottosin, 2014). Ionic homeostasis is the key process that regulates the ion flux of the cell to maintain a low Na^+ ion concentration and build up an optimum K^+ concentration (Han *et al*., 2015; Dabbous *et al*., 2017). The activation of vacuolar H^+-ATPases and H^+-pyrophosphatases facilitates ion extrusion from cells that have been affected by the salinity stress. Salinity stress also affects the expression of certain K^+ genes, both up-and down-regulating them (Assaha *et al*., 2017). The excess Na^+ is compartmentalized in the vacuole as an effective defense against ion toxicity to protect the cytosol from the harmful effects of Na^+ ions (Pottosin *et al*., 2021). This mechanism helps to maintain the K^+/Na^+ ratio in the cytosol and ensures mungbean survival under salinity conditions (Yang *et al*., 2018).

For salt tolerance, transcription factors like NAM (no apical meristem), ATAF (Arabidopsis transcription activation factor), CUC (cup-shaped cotyledon), AP2/ERF (Apetala 2/ ethylene responsive factor), WRKY (W-box binding factor) and basic leucine zipper domain regulate signal transduction and gene expression (bZIP) (Baillo *et al*., 2019; Fraile Escanciano *et al*., 2010). Plasma membrane protein (PMP), salt overly sensitive (SOS), Na^+/H^+ exchangers (NHXs) and high sodium affinity transporter (HKT) are just a few of the genes and transcription factors that control ion transport and exclusion that are activated during salinity stress and help to reduce ion toxicity in cells (Amin *et al*., 2017). All of these transcription factors and genes interact with one another, which helps plants build tolerance mechanisms for salt stress (Xie *et al*., 2022).

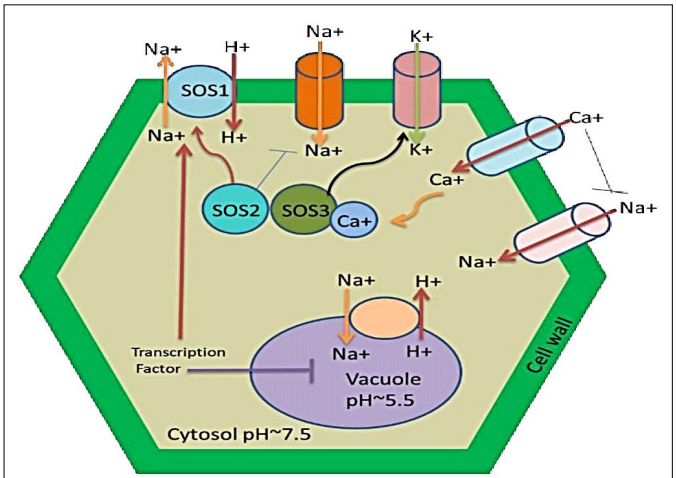
SOS transcription factor one of the most famous TFs regulates several signaling pathways that support a plant's defense against a variety of environmental stresses like salinity. SOS controls Na^+ efflux from plant cells, enhancing ion homeostasis and is the main regulator under salt stress (Ji *et al*., 2013). All the three protein domains of SOS have progressively activated like a cascade wherein SOS1 codes for Na^+/H^+ antiporter in the plasma membrane, SOS2 is a Ser/Thr kinase and SOS3, a Ca^{2+} binding protein that catalyzes Ca^{2+} induced Na^+efflux from the cell and also regulates long-distance transport of Na^+ from root to shoot (Iqbal *et al*., 2020) (Fig 5). In numerous physiological processes, Ca^{2+} ions serve as a crucial second messenger, activating downstream signaling cascades (Liu *et al*., 2021).

Antioxidant defense system

Reactive oxygen species (ROS), high osmotic stress and ion toxicity develop in plants due to excessive salt accumulation in the root zone of plants (Bhattacharjee *et al*., 2019) (Fig 6). The ROS level when reaching a higher concentration in plants causes the oxidation of lipids and protein and degradation and alteration in deoxyribonucleic acid (DNA) sequencing (Rajput *et al*., 2021). Plants resistant to salt stress develop an antioxidative mechanism by activating various enzymes like superoxide dismutase (SOD) and catalase (CAT) (Dumanović *et al*., 2021). From numerous studies from the past, it is clear that the antioxidant defense system manages oxidative damage during abiotic stress in plants. The POX activity in the seedling was drastically elevated (2.78 times) at 300 mM NaCl concentration compared to control in mungbean plants (Farheen *et al*., 2018). Plants have water-soluble antioxidants that make them strongly redox buffered. Electrons react with oxygen molecules to form hydrogen peroxide (H_2O_2) as superoxide radicals. Various enzymes are involved in regulating intracellular H_2O_2. Among these, peroxidase (POX) and CAT are crucial ones (Sachdev *et al*., 2021). Plants increase the production of SOD, which converts O_2 to H_2O_2 and further CAT and POXs catalyze the breakdown of H_2O_2 as part of a sequence of detoxifying mechanisms (Hasanuzzaman *et al*., 2019). Although CAT is absent in the chloroplast, however, H_2O_2 can be detoxified in a reaction catalyzed by an ascorbate-specific peroxidase often present in high levels in this organelle through the ascorbate-glutathione cycle also known as Foyer-Halliwell-Asada pathway (Fig 7) involves the antioxidant metabolites *i.e*., ascorbate, glutathione and NADPH and the enzymes linking these metabolites (Foyer and Noctor, 2011). Various antioxidants such as ascorbic acid (AsA), tocopherol and

Table 1: Type of osmoprotectant production in plants and their roles in osmoregulation.

Class of osmoprotectant	Name	Mechanism of osmoregulation
Amino acids	Alanine, Arginine, Proline, Glycine, Glutamine, asparagine, γ-aminobutyric acid	Precursors for most osmolytesprevent membrane damage and ion toxicity
Quaternary ammonium compounds	Glycine betaine, β-alanine betaine, Proline betaine, Choline-O-sulphate, Hydroxyproline betaine	Protection against damage of membrane, enzyme activity, regulation of ROS detoxification
Tertiary sulphonium compounds	Dimethyl Sulphoniopropionate (DMSP)	Osmoprotection, Detoxifies excess sulphur
Sugars	Sucrose, Trehalose, Fructose, Maltose, Rhamnose	Osmotic adjustment and stabilizing membranes
Sugar alcohols	Pinitol, Mannitol, Myo-inositol, Ononitol, Sorbitol	Facilitates osmoticadjustment and acts as signaling molecules



In response to salinity stress, the SOS pathway (enabling Na^+ efflux), vacuolar sequestration of Na^+ and K^+ inclusion play an important role in inducing salt tolerance in the cells under stress.

Fig 5: Ion homeostasis in response to salt stress.

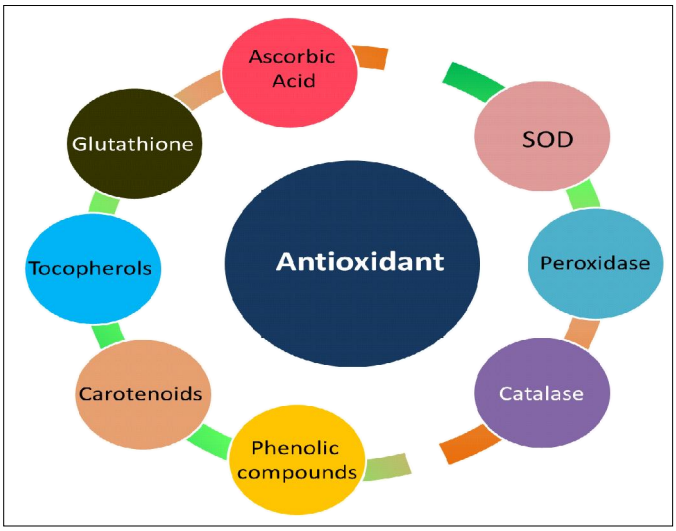


Fig 6: Types of antioxidants.

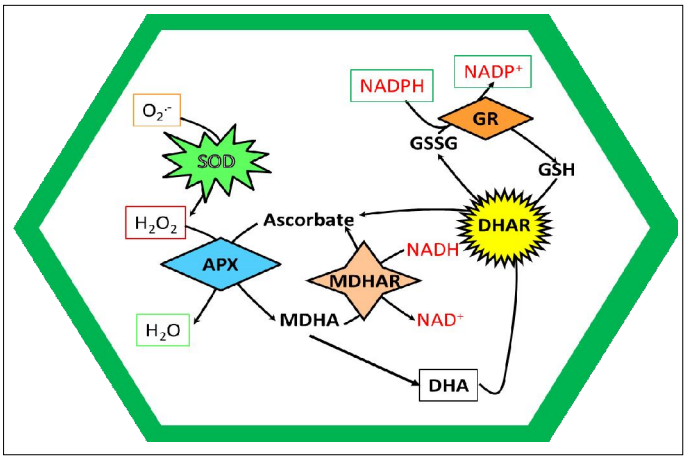


Fig 7: Ascorbate-Glutathione cycle in scavenging ROS.

some phenolic antioxidants are found in mungbean like other plants, which gives protection from oxidative stress. In an experiment conducted by Alharby *et al*. (2019) the salt stress increased the H_2O_2 production under 250 mM NaCl in different genotypes of mungbean. The activity of SOD, CAT, APX, GR, GPX increased significantly upon the NaCl treatments and was maximum at 150 mM for SOD and CAT, at 200 mM for APX, GR and GST and at 250 mM for GPX. In an experiment by Khan *et al*. (2010), similar results were obtained under salt stress. Salt stress increased SOD, GR and APX activity by 30.0%, 8.7% and 35.9%, respectively and glutathione content in NaCl-grown plants increased twice in comparison to the control of mungbean plants. Similar results were obtained by Saha *et al*. (2010) in an experiment conducted on mungbean under NaCl stress, salinity significantly ($P \leq 0.01$) increased the SOD, CAT and POX activity in both roots and leaves over control.

Hormonal regulation

Phytohormones play an important role in various biochemical and physiological mechanisms in plants. They play essential roles in signal transduction pathways during stress response and regulate internal and external stimuli (Jalil and Ansari 2019; Wani *et al*., 2016) (Fig 8). Their role in alleviating abiotic stress is critical in providing tolerance to plants under adverse conditions (Fahad *et al*., 2015). Phytohormones comprise five main groups, namely auxins (IAAs), cytokinins (CKs), abscisic acid (ABA), gibberellins (GAs) and ethylene (ET). Salicylates (SAs), jasmonates (JAs), brassinosteroids (BRs), strigolactones (SLs), polyamines and some peptides represent new families of phytohormones (Khan *et al*., 2020). Several phytohormones interact together, forming a defense network against environmental stresses such as JA, SA and ABA which play a crucial role in regulating signaling pathways (Ryu and Cho, 2015). As the first line of defense, ABA has long been recognized to synthesize roots during soil water deficit. ABA can mitigate the inhibitory effects of salinity on photosynthesis, growth and translocation of assimilates. The positive link of ABA with salinity tolerance is partially credited to K^+, Ca^{2+} levels and compatible solutes in the cytosol, which offset Na^+ and Cl^- uptake, antagonistic interaction between ABA and CK was also revealed during salinity stress, which hinders the tolerance. Through the DELLA (aspartate, glutamate, leucine, leucine, alanine) proteins, GA interacts with ethylene. Ethylene causes DELLA proteins to accumulate more, which reduces the function of gibberellins (Xue *et al*., 2021; Vishal and Kumar, 2018). In comparison to plants where the accumulation of DELLA proteins was not seen, those with higher DELLA protein accumulation demonstrated better tolerance to salinity stress. Additionally, GA may function downstream of ethylene signaling to resist salt stress (Castro-Camba *et al*., 2022; Nawaj *et al*., 2017). The cross talk between auxin and ethylene results in the stimulation of the antioxidation mechanism (Thao *et al*., 2015). Salinity stress leads to water scarcity in plants due to low soil water content and high vapor pressure due to climatic conditions. Because of the lack of water, ABA causes the stomata to close, preventing water loss through transpiration (Chen *et al*., 2022; Ma *et al*., 2020). JA is known to boost photosynthetic activity and lower Na^+ concentration during salt stress, acting as a positive controller of salinity stress tolerance in plants (Delgado *et al*., 2021). Ethylene and JA may either work together or antagonistically in response to stress conditions. The cross talk between JA and ethylene is mediated *via* EIN3/EIL1 along with JAZs MYC2 (Fernando 2020; He *et al*., 2017; Kazan and Manners, 2012). JA and ethylene act synergistically and repress leaf growth and expansion by targeting AUXs which are responsible for the growth and suppressor of JA synthesis (Wasternack and Hause, 2013). BRs also help in avoiding oxidative damage done by ROS

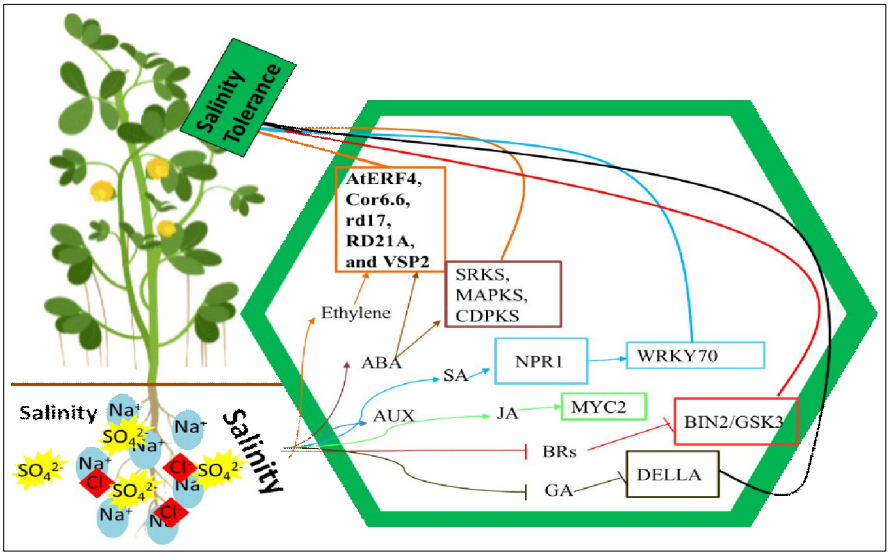


Fig 8: Hormonal regulation for salt stress tolerance.

as it initiates the production of ethylene and ROS, which in turn activates AOX, leading to the detoxification of excess ROS produced. BR and ethylene act synergistically in overcoming the adverse effects of salinity during seed germination (Riyazuddin *et al*., 2020).

CONCLUSION AND FUTURE PROSPECTIVE

Salinity stress is deleterious for the growth of glycophytes and mungbean being a glycophyte suffers a lot from the salinity its growth, development and final yield are all significantly reduced under salinity stress. Complex reactions at the molecular, cellular, metabolic, physiological and whole-plant levels are required for salinity tolerance. In this review, plentiful investigations involving cellular, metabolic and physiological analysis have shown that, among other salinity responses, mechanisms like ion homeostasis, osmotic regulation, antioxidant metabolism and hormonal signaling plays critical roles in plants' capacity to adapt to salinity stress. Nevertheless, there is still much to learn about the changes in the biochemistry of plants under salinity stress, despite the substantial progress made in our understanding of plant stress responses. Future research should concentrate on the molecular interactions between and within cells that contribute to the response to salt stress.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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