ANSF
APPLIED AND NATURAL SCIENCE FOUNDATION

*Journal of Applied and Natural Science*
15(3), 1137 - 1146 (2023)
ISSN : 0974-9411 (Print), 2231-5209 (Online)
journals.ansfoundation.org

*Review Article*

# Salt stress and its impact on rice physiology with special reference to India- A review

**Abinaya Sezhiyan**
Adhiparasakthi Agricultural College, G.B. Nagar, Kalavai, Ranipet- 632506 (Tamil Nadu), India
**Ashok Subiramaniyan***
Adhiparasakthi Agricultural College, G.B. Nagar, Kalavai, Ranipet- 632506 (Tamil Nadu), India
**Chandrasekaran Perumal**
College of Agricultural Sciences, SRM University, Kattankulathur- 603203 (Tamil Nadu), India
**Ashokkumar Natarajan**
College of Agricultural Sciences, SRM University, Kattankulathur 603203 (Tamil Nadu), India
**Rajeshkumar Arumugam**
College of Agricultural Sciences, SRM University, Kattankulathur- 603203 (Tamil Nadu), India
**Kuttimani Ramalingam**
Department of Agronomy, Tamil Nadu Agricultural University, Coimbatore- 641003 (Tamil Nadu), India
**Navin Kumar Chinnaraju**
Department of *Agricultural* Metrology, Vanavarayar Institute of Agriculture, Pollachi – 642103 (Tamil Nadu), India

*Corresponding author. Email: ashok.tnau.ac.in@gmail.com

***Article Info***
https://doi.org/10.31018/jans.v15i3.4747
Received: May 24, 2023
Revised: August 28, 2023
Accepted: September 2, 2023

***How to Cite***

Sezhiyan, A. *et al.* (2023). Salt stress and its impact on rice physiology with special reference to India- A review. *Journal of Applied and Natural Science*, 15(3), 1137 - 1146. https://doi.org/10.31018/jans.v15i3.4747

**Abstract**
With the increasing population, by 2030, the population of India will have seen an unprecedented rise of 1.43 billion and require food grains of around 311 million tones. Of the total area, nearly 5% of the area in India is affected by soil salinity. It is said that about 10% of soil is salinized every year. At this rate, 50% of the land area will be salinized by 2050.These repercussions challenge us to expand the area under cultivation or to increase the yield per unit area to maintain food security and sustainability. In order to meet the growing demands of the increased population, two major approaches can be met. Firstly, the available area under cultivation must be increased, which can be done by the reclamation of various problematic soils and making them suitable for cultivation. The second and holistic approach is to employ various biotechnological and breeding aspects in the development of resistant varieties surviving the harsh and unfavourable environment and showing no subsequent reduction in the yield parameters. For this, one must understand the various physiological aspects of tolerance for screening the elite varieties suited for a particular ecosystem or environment. Thus, the present study vividly explains the various physiological aspects of salt stress on rice. Employing these techniques, one can screen superior genotypes resistant to various stresses, thus keeping the Malthus predictions at bay.

**Keywords:** Genotypes, Population, Sustainability, Salt stress

## INTRODUCTION

Rice, a Kharif crop, has been cultivated as a major staple crop for more than one-third of the world's population for over 11500 years (Joseph *et al.,* 2010). Globally rice is grown mostly in the continents of Asia and Africa. The area and productivity are higher in India globally, but it stands second in rice production than China (Muthayya *et al.,* 2014). The area under rice cultivation in India is 11.92 Lakh Ha. Tamil Nadu has the higher area coverage of 8.73 Lakh Ha followed by Telangana and Andhra Pradesh (2021-22). The other prominent rice-producing states in India are Andhra Pradesh, Kerala and Assam. The other states contribute only about 0.97 Lakh Ha for rice cultivation. The union agricultural ministry had intimated that the area under paddy cultivation has decreased in the past year by 5.62% than in 2021 (Paddy outlook – January 2022). India has achieved self-sufficiency in food production. This is obvious from the fact that the production of food grains

This work is licensed under Attribution-Non Commercial 4.0 International (CC BY-NC 4.0). © : Author (s). Publishing rights @ ANSF.

in India has increased about 5.5 times from 50-250 tones (1950-2017). With the increasing population, by 2030, the population will have seen an unprecedented rise of 1.43 billion and require food grains of around 311 million tonnes. Of the total area, nearly 5% area in India is affected by soil salinity (Kumar *et al.,*2020). It is said that about 10% of soil is salinized every year. At this rate, 50% of the land area will be salinized by 2050 (Muthuramalingam *et al*., 2022).These repercussions challenge us to expand the area under cultivation or to increase the yield per unit area to maintain food security and sustainability.

Abiotic stresses like drought and salinity threaten crop production and the country's food security, reducing the major staple crop yield by more than 50% (Abdallah *et al*., 2016). The Indo-Gangetic plains of India suffer from a marked reduction of 45% in yield due to salt stress (Sampangi-Ramaiah *et al*., 2020). Some studies suggest soil salinity results in a global economic loss of around US $ 27.3 billion per year (Shahid *et al*., 2014). Of the global cultivated land of 800 million hectare, 20 percent of the cultivated land faces the serious threat of salinity. Salinity incurs one-third of the world's total irrigated lands (Dai *et al*., 2022). Soil is considered saline if it has an EC range of $4dSm^{-1}$. Rice is a moderately sensitive crop to salinity. EC of 0 - 8 $dSm^{-1}$ is found to be sensitive to rice. Salinity threshold level and slope are the two important parameters in assessing the salinity tolerance of plants. For rice, the salinity threshold level is 3 $dSm^{-1}$ and the slope is 12%, *i.e.there* is a 12% decrease in yield with every unit increase in EC. Salinity causes a 40% and 14% reduction in root and shoot lengths, respectively (Ling *et al*., 2020). Coastal areas are most prone to salinity due to the problem of saltwater intrusion. The Arid and semi-arid regions are also vulnerable to salinity due to the lower precipitation and higher evaporation rates in these regions (Hussain *et al*., 2013). Rice is considered variably sensitive to salinity at different stages of its growth, starting from seedling emergence to harvest (Kalaiyarasi *et al*., 2019).

**Pokkali– A potent salt-tolerant donor**

Rice is considered a desalinization crop that can reclamate salt-affected soils (Hoang *et al.,* 2016). *Japonica* varieties are more susceptible to salinity than *Indica,* since they are excellent $Na^+$ excluders and they maintain $Na^+$ and $K^+$ homeostasis in the shoot. In the wild variety, Pokkali, a QTL Saltolis, is responsible for maintaining this homeostasis in the shoots of the rice plant. This QTL is situated in Chromosome 1 and confers tolerance to the rice plants at the vegetative stage. For the effective selection of salt-tolerant variety in breeding, there must be proper identification of QTLs for tolerance. In addition to the previously reported saltol that is recently used in breeding programmes. Chen and Jiang (2010) identified 22 QTLs for salt tolerance. Of which 3 QTLs located in chromosomes 1, 4 and 12 pertaining to Salt Injury Score are responsible for transporting $Na^+$ ions from the roots to the shoots. Sri Lanka is the first country to undergo screening and grow salt-tolerant Pokkali rice. Salinity causes a decrease in the starch content if the salt concentration exceeds $4dSm^{-1}$ (Qin and Huang *et al*., 2020).

Pokkali, a traditional rice cultivar, is recognized as the salt-tolerant donor. Though it has some drawbacks, like low tillering capacity, highly prone to lodging, and poor cooking quality, this cultivar is considered a salt-tolerant gene donor in classical breeding. It showed an increase in its plant biomass (approximately doubled) and undersalt stress (Joseph *et al*., 2010). Recent studies have suggested that endophytes confer tolerance to various biotic and abiotic stresses. Sampangi-Ramaiah *et al*. (2020)identified a salinity-tolerant endophyte in a study pertaining to the salt-tolerant Pokkali rice, i.e. *Fusarium spp*. This endophyte was inoculated in the salt-sensitive indica variety IR64. This endophyte-colonized rice seedlings showed a pronounced increase in growth and salt-tolerant parameters.

**Mechanism of salt tolerance**

The majority of plants come under the classification of glycophytes and only about one percent comprises halophytes, tolerating a salt concentration of around 300 - 1000mM. Halophytes can compartmentalize the excess sodium ions to accumulate enough quantity of osmolytes and to maintain potassium ion homeostasis. Glycophytes tend to have resistance mechanisms aiming to survive rather than to reproduce or grow during stress conditions. Dai *et al*. (2022) inferred that the toxic effects of salt stress are seen under four aspects: oxidative stress, osmotic stress, nutritional deficiency, and ionic stress. The two main problems the plants grown under salt conditions face are physiological water deficit (osmotic stress) and ion toxicity. Oxidative stress become significant in the plant only in the later stages after the osmotic stress and ion toxicity becomes prominent. Osmotic stress occurs due to the reduced soil water potential due to the accumulation of solutes like $Na^+$ and $Cl^-$, making it difficult for the plant roots to absorb nutrients and water from the soil.

To maintain normal conditions, plants must decrease the cytosolic water potential to aid in the uptake of water and nutrients. For this, plants must accumulate organic solutes in their cytosols. Or the plant must enhance the influx of inorganic ions from the soil and sequester them in the vacuoles and even in organelles like mitochondria and Golgi bodies (Kader *et al*., 2011). Salt exclusion is the major salt tolerant mechanism found in halophytes, of which the mangroves have the ability to exclude 99% salt through the roots . Morphologically, plants can tolerate stress by increasing succulence, reducing the size and number of leaves, leaf

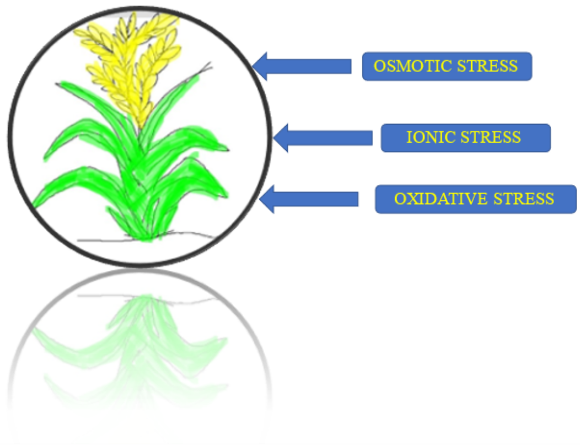


**Fig. 1.** *Effect of salinity stress on rice*

cuticle thickening, root lignifications etc. The increase in succulence is correlated with the increase in cell size. The increase in cell-size provides more space for the accumulation of toxic ions like $Na^+$ and $Cl^-$. Halophytes possess special structures like glands, trichomes, and bladders for the selective exclusion and inclusion of ions. The wild rice, *Oryza coarctata Roxb* has been found to possess salt glands (Yadav *et al*., 2011).

### Salinity induced osmotic stress

It is inferred that the osmotic stress causes major yield losses in plants even before the foliar symptoms become evident (Yadav *et al*., 2010). Osmotic stress is the initial effect of salt-related stresses, mostly due to the reduction in the soil water potential by the high concentrations of Na+ and Cl- ions (Hossen *et al*., 2022). Normally, plants can absorb water and nutrients required for their growth and development from the soil, provided the osmotic pressure of the plant system tends to be higher than that of the soil solution (Fig. 1). But due to salinity, there occurs an increase in salt concentration, drastically increasing the osmotic pressure of the soil solution, making it difficult for the plants to absorb their daily requirements from the soil (Kader *et al*., 2010). The restriction in the absorption of the plant's daily requirements from the soil culminates in the reduction of the photosynthesis rate, transpiration and growth of plant. The reduction in transpiration and photosynthesis is due to their effects on the stomatal opening and stomatal conductance owing to the salinity stress effects on the size and density of the stomata. (Muthuramalingam *et al*., 2022). Among cereals, rice is more sensitive to salinity. To be secured during such hyperosmotic stress, plants have developed mechanisms like the sequestration of organic solutes or compatible solutes (osmoprotectants) and inorganic ions to compensate the reduced osmotic potential of the cell components (Joseph *et al*., 2010). Trehalose is found to play a critical role in defending plants against many abiotic stresses than Proline (Mostofa *et al.,* 2014). These compatible solutes are low-molecular weight compounds that do not affect the plants' normal physiological and biochemical reactions. The compatible solutes produced in the plants include sugars (glucose, sucrose, fructose, trehalose), polyols (mannitol, sorbitol) nitrogen-containing compounds (NCC) viz. amino acids (proline, glutamate), proteins, polyamines, amides, quaternary ammonium compounds like glycine betaine. Tolerance to salt and related stresses is positively correlated with an increase in the concentration of such compatible solutes. In rice, reports show increased proline levels in the leaves and glycine betaine biosynthesis under stress conditions (Safdar *et al*., 2019). These compatible solutes also help reduce free radical accumulation and in osmotic adjustment (Chen and Ziang, 2010). Organic solutes are produced and accumulated in the cytosols as a counter-effect of osmotic stress. Such a mechanism is seen mostly in plants that are included in the glycophyte classification. And the accumulation of high concentrations of inorganic ions like Na+, K+, Ca2+, and Cl– to check the movement of ions is present in halophytes.

### Osmotic adjustment

In response to the stress, plants accumulate the organic solutes or compatible solutes in their cytoplasm by which the cell turgor is restored and the water potential is decreased, thereby facilitating the easy uptake of water and nutrients from the soil solution. These solutes also aids in decreasing the ion toxicity, giving the plants protection against osmotic stress and thus providing tolerance to salt and drought stress. The mechanism of osmotic adjustment also includes the reduced influx of Na+ or sequestering of the excess ions in compartments. The major organic and inorganic solutes that accumulate in the plant system are discussed below.

### Organic osmolytes

Glycine betaine is a quaternary ammonium compound synthesized in the chloroplast involving many enzymes. They play a pivotal role in decreasing plants' Na+/K+ and Na+/Ca2+ ratios. They also increase the production of vacuoles in the roots of plants under salt stress for the accumulation of Na+ ions. Vacuoles are essential during salt stress in compartmentalizing the excess Na+ and Cl- ions, reducing the toxic effect of such ions and aiding in osmoregulation since it occupies about 95% of the cell space (Kader *et al.,* 2010). This facilitates the decrease in the plants' water potential, making it easy for the plants to absorb water and nutrients from the soil. It aids in osmoregulation, scavenging free radicals, and protects the chloroplast from any damage under stress. In rice seedlings, the damages caused by salinity, like disruption in the activities of cell organelles like chloroplast and mitochondria, can be reduced by glycine-betaine (Choudhary *et al.,* 2022).

Proline, an amino acid, helps plants to adjust osmosis by accumulating in the cytosol under salt and drought stress. Plants also produce various sugar alcohols (mannitol, pinitol) in response to osmotic stress. In a recent study conducted in the wild rice relative *Oryza coarctata*, showed the accumulation of pinitol, a cytosolic sugar that aids in conferring tolerance against various stresses. It also aids in maintaining the integrity of cell membranes and enzymes, thus behave as an osmoprotectant (Mishra *et al*., 2022). The total soluble sugars and tolerance to salt stress is positively correlated in rice plants i.e. the increase in the accumulation of such cytosolic sugars like trehalose, glucose, sucrose and fructose aids in the restoration of the osmotic potential and thus conferring tolerance to plants(Cha-um *et al*., 2009). Among the sugars, trehalose plays a key role in imparting tolerance to salt stress. It is inferred that, under osmotic stress, Trehalose is found to be more beneficial than proline. Exogenous Trehalose application conferred considerable tolerance against oxidative stress by mediating the production of antioxidants to keep the levels of free radicals in check (Abdallah *et al*., 2016). Under salt and heat stress, the levels of $H_2O_2$ and MDA were found to be decreased in rice and wheat seedlings, respectively with the exogenous application of Trehalose (Mostofa *et al.,* 2014). Glycerol is an effective osmolyte in imparting osmotic balance owing to its easy synthesis from glucose, quicker solubility etc. (Chen and Ziang *et al*., 2010).

**Inorganic ions**

Even at lower concentrations, the accumulation of inorganic ions is metabolically feasible than the production of organic solutes (Patakas *et al*., 2002). To maintain a proper cell turgor, cell osmotic potential and the normal functioning of essential enzymes, cytosolic potassium concentration must be about 100-200 mM, whereas the concentration of cytosolic sodium should be maintained at not more than 10mM (Safdar *et al*., 2019). Cytosolic Calcium triggers signal transduction cascades in response to stress (Kader *et al*., 2010). Owing to its many beneficiary roles in rice plants under abiotic stresses like drought and salinity, viz. increasing the photosynthetic rates, plant's antioxidant activity and leaf water potential, the external supplementation of Calcium confers tolerance to plants against various abiotic stresses (Rahman *et al*., 2016 and Nedjimi *et al*., 2017). Diédhiou *et al*., 2006 observed a rapid increase in Cl- ion concentration under stress in salt-sensitive lines viz. IR29 probably contributes to cellular osmoregulation and restoring the cell turgor under salt stress. The glycophytes and halophytes can accumulate these compatible solutes at a concentration of about 40 and 10 mM (tissue water basis), respectively. Among the inorganic ions, K+ contributes about 63% towards osmoregulation in the shoot cells (Choudhary *et al*., 2022).

**Disruption in ion homeostasis**

Plants need micro and macro mineral nutrients for their growth and development. But, under salinity conditions, due to the hyperaccumulation of toxic ions like Na+ and Cl-, an ionic imbalance or a disruption in the ion homeostasis occurs. The abrupt increase in such toxic ions during stress affects the nutrient availability and their movements in and out of the plants. This, in turn culminates in nutrient deficiency in plants under stress. The toxic ions like Na+ and Cl- compete with mineral nutrients like K+, Ca2+, Fe+, Mg2+. Potassium ions aid in the maintenance of osmotic balance and in decreasing ion toxicity. In rice plants, the K+/Na+ ratio positively correlates with the plant's tolerance to salinity. Salinity exposed plants are also prone to Fe deficiencies because of the formation of iron complexes, making it unavailable for the plants (Islam *et al*., 2019). Iron, a micronutrient, is a component of many enzymes, aiding in many physiological processes like photosynthesis, transpiration and nitrogen fixation.

The availability of Fe is reduced at pH less than 5, making it unavailable when soil is exposed to salt or sodic conditions. Abbas *et al*. (2015) showed that the salinity and Fe deficiency in combination are detrimental to the growth of rice cultivars, reducing the dry weights of shoot & root. Fe deficiency also resulted in a decrease in chlorophyll concentration and the photosynthetic rate. The restricted release of Phytosiderophores by Salinity exposed cells, limits the availability of Fe to the plants. Hasanuzzaman *et al*. (2017) showed the importance of micronutrients in stress alleviation. For instance, Silicon (Si) and Selenium(Se) micronutrients are key in mitigating salt stress in salinity-exposed rice plants. External application of Si and Se confers salt-stress tolerance in rice.

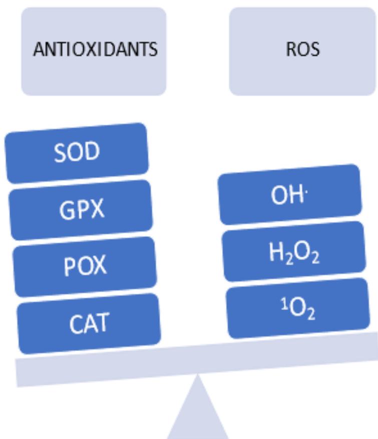


**Fig. 2.** *Equilibrium between the antioxidants and ROS*

| ENZYMATIC DEFENSE SYSTEM | NON ENZYMATIC DEFENSE SYSTEM |
|---|---|
| CAT, SOD, POX, GPX, APX, GR | Glutathione, Ascorbic acid, flavonoids, carotenoids, proline,α tocopherol |

**Fig. 3.** *Various enzymatic and non enzymatic defense systems prevalent in rice*

The Increase in Na+ toxicity in plants under salinity is due to the antagonistic effect of Na+ over K+ (Islam *et al*., 2019). There occurs a competition between these two cations. Under salinity, Na+ accumulates in the plants' roots, inhibiting the uptake of K+ affecting various enzyme activities. This is because K+ is found to be responsible for regulating about 50 enzymes (Kader *et al*., 2010). This causes an ionic imbalance in the cells, affecting the cellular metabolism. A positive correlation occurs between the Na+ exclusion and the plants' tolerance against salinity. When the plant senses some stress, the cytosolic calcium increases, triggering many signal transduction pathways. When exposed to stress, it acts as a secondary messenger molecule during various plant growth and development processes (Kader *et al*., 2010). The balance between the quantity of micro and micronutrients is greatly affected by salinity. Elements like Na and Zn were higher, and P and Mn were decreased under salinity (Yang et al., 2023).

**Salinity-induced oxidative stress**

Oxidative stress is the finaland prominent effect of any salt-related stress. The oxidative stress caused due to the superfluous accumulation of the reactive oxygen species becomes significant in plants only after the occurrence of osmotic and ionic stress (Fig. 2). The oxygen molecule that is used by plants and other living beings in the electron transport chain is transformed into Reactive Oxygen Species (ROS). These ROS are mere excited or partially reduced forms of oxygen (Kerchev *et al*., 2022). Plants produce reactive oxygen species under stress conditions. ROS are produced by plants when an unfavourable condition occurs in the cytosolic or peroxisomal atmosphere. They are cytotoxic materials that react with various biomolecules in the plant system, like proteins, lipids, and nucleic acids. These reactions, in turn, result in the peroxidation of lipids, denaturation of proteins or amino acids and causes damage to the double-stranded structure of the DNA (Monsur *et al*., 2022). The ROS also causes many deleterious effects on the cell. The structure of the chloroplast deteriorates when exposed to salinity which is mainly associated with salt-induced oxidative stress. In rice, the thylakoids show swelling due to the over-accumulation of $H_2O_2$ under salinity.$H_2O_2$ has a longer half-life than other ROSs (Liang *et al*., 2015). The deterioration in the structure of the chloroplasts tends to be the main reason for the decreased photosynthetic rates in salt-exposed plants (Islam *et al*., 2019). ROS are nothing but species of Oxygen having higher affinity to electrons, thus damaging the biomolecules (Mansoor *et al*., 2021). ROS also acts as signaling molecules during stress, essential in regulating the oxidative stress in plants caused by various abiotic and biotic stresses like drought, salinity, and pest and disease attack. They become dangerous to plant growth and development once they surpass their limit. There always exists a subtle equilibrium between the ROS and the antioxidants in the plant system, which is crucial in conferring tolerance. The transition from this equilibrium, *i.e.,* the production of ROS outweighs the production of the antioxidants, is the main reason plants are prone to the ill effects of oxidative stress (Gill and Tuteja 2010). About 1-2% of the Oxygen taken by the plants from the atmosphere is shunted to ROS production (Gill and Tuteja 2010). ROS is contemplated as the double-edged sword of life (Mansoor *et al*., 2021) since it is crucial in maintaining the balance between the ROS and antioxidants thus regulating oxidative stress. Plant stress induces ROS production, which activates the signal transduction cascade to cope with the prevailing undesirable environment (Ansari *et al*., 2021). As opposed to this, they cause numerous menacing effects to the plants, like cell death, including ferroptosis or necrosis. The sites of ROS production are the organelles with high activities of oxidizing metabolism, like the chloroplast, peroxisome and mitochondria (Monsur *et al*., 2022).

Rice being a C3 plant, the photorespiration occurs at a higher rate, leading to the low rate of $CO_2$ fixation. This low availability of $CO_2$ coerces the RUBP oxygenase enzyme to use O2 to catalyze the reaction, producing glycolic acid. This glycolic acid is oxidized to $H_2O_2$ and glyoxylic acid. This reaction is catalyzed by the enzyme glycolate oxidase in the peroxisome, which is the major production site of free radicals or reactive oxygen species. The levels of glycolate oxidase in the plants remain a parameter in assessing the tolerance to oxidative or salt stress. The $H_2O_2$ metabolism is the principal source of other harmful free radicals, which tend to be higher in rice due to the reduced action of the enzyme glyoxylate – glutamate Aminotransferase, which is involved in the conversion of glyoxylate to amino acids like glycine and serine (Singha *et al*., 1990). The same situation prevails in the plant system at times of stress, where a disturbance in the K+ homeostasis occurs due to the $Na^+$ toxicity. Potassium ions are essential in the leaf's photosynthetic and respiratory activities, aiding in the opening and closing of the guard cells during respiration and photosynthesis. This non-availability of $K^+$ ions restricts the opening of the guard cells, causing dehydration of the plants, causing osmotic stress. The respiration or the intake of $CO_2$ is also affected. This, in turn, causes an increase in the production of $H_2O_2$ during stress. The ROS can be of radical or non-radical forms viz. Superoxide radicals $•O_{2-}$, hydroxyl radicals •OH, per hydroxyl radicals ($HO_{2-}$) and hydrogen peroxide ($H_2O_2$) and singlet oxygen ($^1O_2$), respectively (Rajput *et al.* 2021). Oxidative burst also measures the increase in Malondialdehyde's activities in rice seedlings' shoots (Pharmawati *et al*., 2019).

### Detoxification of ROS

In detoxifying the ill and deleterious effects of the ROS, plants accumulate various antioxidants, viz. enzymatic and non-enzymatic. The rice variety Pokkali which is used as a check variety as indicated by the International Rice Research Institute (IRRI), shows the highest activity of antioxidants viz. catalase (CAT), ascorbate (ASC), glutathione (GSH) when exposed to salt stress (Hoang *et al*., 2016). The first line of defense is the plant production of antioxidants; the second line of defense involves the increased activity of the primary genes by hormone-mediated signaling pathways like GABA shunt for the expression of genes (Ansari *et al*., 2021). The different mechanisms that assist in the detoxification of ROS are more effective at the early vegetative stages of the rice plant (Moradi *et al*., 2007). Under stress GABA (gamma amino butyric acid) shunt induces the $Ca^{2+}$ signalling in the cytosol, enhancing the defence against stress by bringing down the activities of ROS (Ansari *et al*., 2021).

### Enzymatic defense system

Plants produce various enzymes to catalyze the detoxification of ROS like catalase (CAT), glutathione, ascorbate, superoxide dismutase (SOD) (Fig. 3). These enzymes show specificity in their actions. Noreen *et al*., 2021 infers that the antioxidant activities significantly increased by providing foliar fertigation of ascorbic acid (Vitamin C) and Zinc. The experiment also showed a corresponding increase in morphological and physiological parameters that confers salinity tolerance in barley. The action of enzymes like SOD, CAT, POX, GPX prevents the Haber Weiss reaction, where hydrogen peroxide reacts with superoxide, forming large quantities of hydroxyl radicals (Rajput *et al*., 2021). The antioxidants found abundant in rice are APX and GR. Under salinity the plant system showed a marked increase in enzymes like glycolate oxidase and decrease in the enzyme activities of SOD and CAT. SOD reduces the toxic effects of ROS by dismutating the superoxide to oxygen and hydrogen peroxide. There are three isoforms of SOD classified based on their metal cofactor viz. MnSOD, FeSOD and the cytosolic Cu/ZnSOD (Gratão *et al*., 2005).

The enzyme CAT mediates the conversion of H2O2 to oxygen and water. The enzyme causing the lipid peroxidation, viz. lipoxygenase (LOX), is inferred as an important enzyme to assess the oxidative stresses in plants (Mostofa *et al*., 2014). The growth of root shows a marked decline when exposed to salt stress due to the increased $H_2O_2$ levels. The NaCl treatment showed a marked increase in certain enzymes like APX and GRbut the activities of enzymes like SOD and CAThad null effect (Joseph *et al*., 2010). Plants produce these enzymes individually or in combinations during any abiotic or biotic stress in reducing the cytotoxic effects of various harmful compounds produced under stress conditions. These significant antioxidants or scavenging enzymes can be pyramided in the production of salt -tolerant rice crops to increase productivity and to achieve food security (Gill and Tuteja 2010).

The Asada–Halliwell pathway or the Ascorbate-Glutathione pathway is considered the major metabolic pathway involved in regulating oxidative stresses caused by the over-accumulation of ROS (Raja *et al*., 2022). APX, MDHAR, DHAR, and GR are the key enzymes involved in this pathway (Hasanuzzaman *et al*., 2019). It also includes the non-enzymatic water-soluble antioxidants viz. Glutathione and ascorbic acid are important in salinity stress alleviation (Kerchev *et al*., 2022). Under stress, all living organisms, from small microorganisms to humans, produce a highly cytotoxic compound, Methylglyoxal (MG) synonymous to the ROS, in causing damage to the cell membrane, affecting its permeability and leading to the leakage of electrolytes (Ghosh *et al*., 2022). The MG is produced as a byproduct of glycolysis. The reduced glutathione (GSH) -dependent glyoxalase pathway plays a pivotal role in detoxifying methylglyoxal's destructive effect. The plant system showed an increase in the enzymes GLYI and GLYII at times of salt stress. In rice, the gene GLYII is found to confer tolerance against salinity in nullifying the effect of MG and other ROS that cause adverse effects to the plant system (Liu *et al*., 2022).

### Non enzymatic defense system

This classification of antioxidants includes water-soluble antioxidants like glutathione and ascorbic acid. It also includes low molecular antioxidants like carotenoids, α-tocopherol, proline, flavonoids etc. (Mansoor *et al*., 2021). GSH (Glutathione) increases the ability of the plants to tolerate metal-induced oxidative stress (Gill and Tuteja, 2010). Due to their significance in the plant defense system under stress, it is considered a potential stress marker in plants (Gratão *et al*., 2005). GSH is not only involved in the disintegration of ROS but also in maintaining the normal physiological functioning of the plants, like regulating the redox, maintaining cellular homeostasis and cellular signaling etc. AsA are known to be potent ROS scavengers owing to their

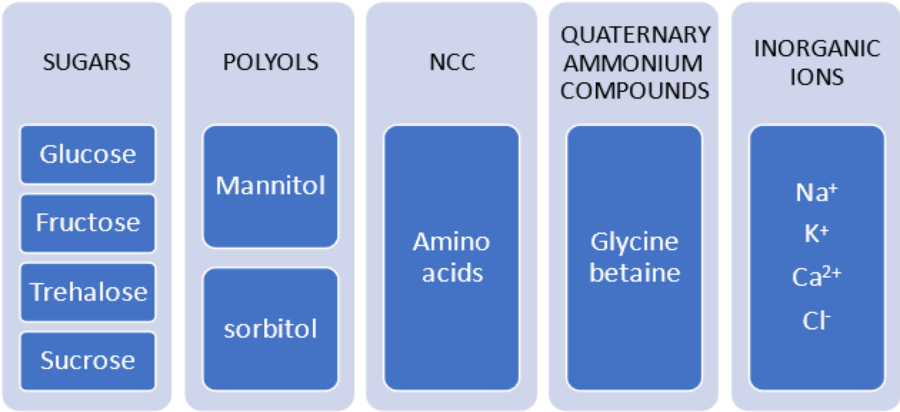


**Fig. 4.** *Different classes of non-enzymatic antioxidants*

ability to donate electrons to the electron-loving ROS (Gill and Tuteja 2010). Mitochondria are considered to be an integral part of the AsA metabolism. AsA are also involved in tocopherol production (Mansoor *et al*., 2021). Under salinity-induced osmotic stress, rice plants showed an increase in AsA which is correlated with the subsequent increase in enzymes like CAT, SOD etc. (Monsur *et al*., 2022). AsA scavenges many free radicals by serving as a substrate and cofactor for many enzymes like peroxidase (Kerchev *et al*., 2022).
Proline is considered to be a potent non-enzymatic antioxidant owing to their role in the inhibition of PCDs. Proline has been found to be the major scavenger of hydroxyl radicals as compared to other osmoprotectants like sorbitol, mannitol and myo-inositol (Fig. 4). Due to its dual properties in alleviating both osmotic and oxidative stress by scavenging free radicals, proline is considered an important non-enzymatic antioxidant (Gill and Tuteja 2010). α-tocopherol (Vitamin E) are fat-hating antioxidants found in the chloroplasts of plant cells and most importantly in the thylakoid membranes. The significance of these antioxidants is obvious from the fact that a mere one-mole α-tocopherol scavenges the superoxide radicals of up to 120 moles. Carotenoids also play a key role in non-enzymatic detoxification of ROS. By the genetic manipulation of the endosperm-specific pathways, the carotenoid synthesis in transgenic golden rice showed a marked increase (Monsur *et al.,* 2022). Recently, golden rice 2 evolved with a β-carotene content up to 37 μg/g in the endosperm (Rezvi *et al*., 2022). The non-enzymatic antioxidant system also includes non-protein amino acids, phenolic compounds, alkaloids etc.

**Other morphological and physiological responses**

Salinity affects rice crops morphologically by reducing the various growth parameters of rice like shoot and root growth, number of tillers, leaf area etc. and causing stunting. Due to its effects on the photosynthetic pigments, the plant shows symptoms of leaf burning. Salinity causes the accumulation of sugars on the shoots and starch on the roots. Physiologically salinity causes damage to the photosynthetic pigments and induces stomatal closure to alleviate stress (Nagarajan *et al*., 2022). The structure of the chloroplast deteriorates when exposed to salinity which is mainly associated with salt-induced oxidative stress. In rice, the thylakoids show swelling due to the overaccumulation of $H_2O_2$ under salinity. The deterioration of the ultrastructure of the chloroplasts tends to be the main reason for the decreased photosynthetic rates in salt-exposed plants (Islam *et al*., 2019).

**Plant hormones in salinity stress**

It is inferred that in comparison with the other major ROS produced in the plant cells, $H_2O_2$ tend to have a longer half-life. Melotonin is an important scavenger of free radicals. As a result of salt and related stresses, plant cells produce free radicals like $H_2O_2$ which causes cell degradation, leading to leaf senescence. This leaf senescence can be delayed in plants by the accumulation of melatonin, which scavenges the $H_2O_2$ (Liang *et al*., 2015). There is also other prominent hormones like ethylene, which helps in the alleviation of salt stress in plants.This is mediated by encouraging antioxidant activity and maintaining ion homeostasis, thus conferring tolerance against salt stress (Riyazuddin *et al*., 2020). But ethylene leads to salinity hypersensitivity in rice, causing a reduction in growth and yield, affecting grain filling and spikelet growth. The external application of Jasmonic acid tends to increase the tolerance against salinity in rice plants. Seed priming with Ethephon with a suitable ethylene inhibitor like 1-MCP can help increase the germination rates in rice seedlings under salt stress (Hussain *et al*., 2020). But some studies also suggest that ethylene negatively impacts rice seedlings (Qin and Huang 2020). The plant hormone ABA has the same impact on rice seedlings as ethylene since there occurred a marked build-up in the antioxidants activity and the ionic balance is maintainedthus conferring salt tolerance (Chen *et al*., 2022). Nitric oxide, another plant hormone, is significant in breaking the dormancy and inducing germination in rice by elevating the rate of abscisic acid catabolism (Yi *et al.,* 2022).

## Conclusion

Salt and drought are the two major stressors to which rice crops are exposed. It is estimated that about 10% of the land is salinized every year. At this rate, about 50% of soil will be attributed to salinity by the year 2050. This poses a serious threat to the food security of India. Rice, a major staple crop grown worldwide, is highly sensitive to salt at the seedling and flowering stage. The population increases drastically, but food is insufficient to feed the growing population. To meet the food requirements of this unprecedented population growth and to keep the Malthus predictions at bay, researchers must find a holistic way to increase the production of food crops. Since the net available area cannot be increased and only tends to decrease with urbanization, scientists must find ways to increase the productivity of food crops, forcing us to grow food crops even in problematic soils without the subsequent reduction in yield parameters. Rice, a saline-sensitive crop, shows a marked reduction in yield if exposed to the salinity of 7.2dS$m^{-1}$. Considering these predictions, scientists must screen the available rice cultivars and involve genetic engineering studies in manipulating the crop to grow even in stressed conditions. If exposed to salinity, there are many physiological effects on rice crops, which should be thoroughly studied and understood for the screening of salt-tolerant varieties that could be a milestone in the future.

## Conflict of interest

The authors declare that they have no conflict of interest.

## REFERENCES


1. Abbas, G., Saqib, M., Akhtar, J. &Haq, M. A. U. (2015). Interactive effects of salinity and iron deficiency on different rice genotypes. Journal of Plant Nutrition and Soil Science, 178(2), 306-311. https://doi.org/10.1002/jpln.201400358
2. Abdallah, M. S., Abdelgawad, Z. A. & El-Bassiouny, H. M. S. (2016). Alleviation of the adverse effects of salinity stress using trehalose in two rice varieties. South African Journal of Botany, 103, 275-282. https://doi.org/10.1016/j.sajb.2015.09.019
3. Ansari, M. I., Jalil, S. U., Ansari, S. A. & Hasanuzzaman, M. (2021). GABA shunt: a key-player in mitigation of ROS during stress. Plant Growth Regulation, 94, 131-149. https://doi.org/10.1007/s10725-021-00710-y
4. Cha-Um, S., Charoenpanich, A., Roytrakul, S. & Kirdmanee, C. (2009). Sugar accumulation, photosynthesis and growth of two indica rice varieties in response to salt stress. Actaphysiologiaeplantarum, 31, 477-486. DOI 10.1007/s11738-008-0256-1
5. Chen, G., Zheng, D., Feng, N., Zhou, H., Mu, D., Zhao, L., … & Huang, A. (2022). Physiological mechanisms of ABA-induced salinity tolerance in leaves and roots of rice. Scientific Reports, 12(1), 1-26. https://doi.org/10.1038/s41598-022-11408-0
6. Chen, H. & Jiang, J. G. (2010). Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environmental Reviews, 18(NA), 309-319. https://doi.org/10.1139/A10-014
7. Choudhary, S., Wani, K. I., Naeem, M., Khan, M. M. A., &Aftab, T. (2023). Cellular responses, osmotic adjustments, and role of osmolytes in providing salt stress resilience in higher plants: Polyamines and nitric oxide crosstalk. Journal of Plant Growth Regulation, 42(2), 539-553. https://doi.org/10.1007/s00344-022-10584-7
8. Dai, L., Li, P., Li, Q., Leng, Y., Zeng, D. & Qian, Q. (2022). Integrated multi-omics perspective to strengthen the understanding of salt tolerance in rice. International Journal of Molecular Sciences, 23(9), 5236. https://doi.org/10.3390/ijms23095236
9. Diédhiou, C. J. & Golldack, D. (2006). Salt-dependent regulation of chloride channel transcripts in rice. *Plant Science,* 170(4), 793-800. https://doi.org/10.1016/j.plantsci.2005.11.014
10. Ghosh, A., Mustafiz, A., Pareek, A., Sopory, S. K., &Singla□Pareek, S. L. (2022). Glyoxalase III enhances salinity tolerance through reactive oxygen species scavenging and reduced glycation. PhysiologiaPlantarum, 174(3), e13693. https://doi.org/10.1111/ppl.13693
11. Gill, S. S., &Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant physiology and biochemistry, 48(12), 909-930. DOI:10.1016/j.plaphy.2010.08.016
12. Gratão, P. L., Polle, A., Lea, P. J., &Azevedo, R. A. (2005). Making the life of heavy metal-stressed plants a little easier. Functional plant biology, 32(6), 481-494. https://doi.org/10.1071/FP05016
13. Hasanuzzaman, M., Bhuyan, M. B., Anee, T. I., Parvin, K., Nahar, K., Mahmud, J. A., & Fujita, M. (2019). Regulation of ascorbate-glutathione pathway in mitigating oxidative damage in plants under abiotic stress. Antioxidants, 8(9), 384. https://doi.org/10.3390/antiox8090384
14. Hoang, T. M. L., Tran, T. N., Nguyen, T. K. T., Williams, B., Wurm, P., Bellairs, S., &Mundree, S. (2016). Improvement of salinity stress tolerance in rice: challenges and opportunities. Agronomy, 6(4), 54. https://doi.org/10.3390/agronomy6040054
15. Hossen, M. S., Karim, M. F., Fujita, M., Bhuyan, M. B., Nahar, K., Masud, A. A. C., … &Hasanuzzaman, M. (2022). Comparative physiology of indica and japonica rice under salinity and drought stress: An intrinsic study on osmotic adjustment, oxidative stress, antioxidant defense and methylglyoxal detoxification. Stresses, 2(2), 156-178. https://doi.org/10.3390/stresses2020012
16. Hussain, M., Park, H. W., Farooq, M., Jabran, K., & Lee, D. J. (2013). Morphological and Physiological Basis of Salt Resistance in Different Rice Genotypes. International Journal of Agriculture & Biology, 15(1).
17. Hussain, S., Zhu, C., Huang, J., Huang, J., Zhu, L., Cao,

X., & Zhang, J. (2020). Ethylene response of salt stressed rice seedlings following Ethephon and 1-methylcyclopropene seed priming. Plant Growth Regulation, 92(2), 219-231. https://doi.org/10.1007/s10725-020-00632-1

18. Islam, F., Wang, J., Farooq, M. A., Yang, C., Jan, M., Mwamba, T. M., … & Zhou, W. (2019). Rice responses and tolerance to salt stress: deciphering the physiological and molecular mechanisms of salinity adaptation. In Advances in rice research for abiotic stress tolerance (pp. 791-819). Woodhead Publishing. https://doi.org/10.1016/B978-0-12-814332-2.00040-X
19. Joseph, B., Jini, D., & Sujatha, S. (2010). Biological and physiological perspectives of specificity in abiotic salt stress response from various rice plants. Asian J. Agric. Sci, 2(3), 99-105.
20. Kader, M. A., & Lindberg, S. (2010). Cytosolic calcium and pH signaling in plants under salinity stress. Plant signaling & behavior, 5(3), 233-238. https://doi.org/10.4161/psb.5.3.10740
21. Kalaiyarasi, R., Kuralarasan, V., George, J., Praveen, N. M., &Manikandan, V. (2019). Salinity tolerance screening in local rice varieties of Tamil Nadu and Kerala. IJCS, 7 (4), 1667-1671.
22. Kerchev, P. I., & Van Breusegem, F. (2022). Improving oxidative stress resilience in plants. The Plant Journal, 109(2), 359-372. https://doi.org/10.1111/tpj.15493
23. Kumar, P., & Sharma, P. K. (2020). Soil salinity and food security in India. Frontiers in Sustainable Food Systems, 4, 533781. https://doi.org/10.3389/fsufs.2020.533781
24. Liang, C., Zheng, G., Li, W., Wang, Y., Hu, B., Wang, H., … & Chu, C. (2015). Melatonin delays leaf senescence and enhances salt stress tolerance in rice. Journal of pineal research, 59(1), 91-101. https://doi.org/10.1111/jpi.12243
25. Ling, F., Su, Q., Jiang, H., Cui, J., He, X., Wu, Z., … & Zhao, Y. (2020). Effects of strigolactone on photosynthetic and physiological characteristics in salt-stressed rice seedlings. Scientific Reports, 10(1), 6183. https://doi.org/10.1038/s41598-020-63352-6
26. Liu, S., Liu, W., Lai, J., Liu, Q., Zhang, W., Chen, Z., … & Xiao, Y. (2022). OsGLYI3, a glyoxalase gene expressed in rice seed, contributes to seed longevity and salt stress tolerance. Plant Physiology and Biochemistry, 183, 85-95. https://doi.org/10.1016/j.plaphy.2022.04.028
27. Mansoor, S., Ali Wani, O., Lone, J. K., Manhas, S., Kour, N., Alam, P., … & Ahmad, P. (2022). Reactive oxygen species in plants: from source to sink. Antioxidants, 11 (2), 225. https://doi.org/10.3390/antiox11020225
28. Mishra, S., Chowrasia, S., &Mondal, T. K. (2022, August). Dhani (Oryzacoarctata): A Wild Relative of Rice is a Potential Source of Coastal Salinity Tolerance Genes Suitable for Rice Breeding. In Transforming Coastal Zone for Sustainable Food and Income Security: Proceedings of the International Symposium of ISCAR on Coastal Agriculture, March 16–19, 2021 (pp. 23-34). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-95618-9_2
29. Monsur, M. B., Datta, J., Rohman, M. M., Hasanuzzaman, M., Hossain, A., Islam, M. S., … &Sabagh, A. E. (2022). Saline Toxicity and Antioxidant Response in Oryza sativa: An Updated Review. Managing Plant Production Under Changing Environment, 79-102. https://doi.org/10.1007/978-981-16-5059-8_4
30. Moradi, F., & Ismail, A. M. (2007). Responses of photosynthesis, chlorophyll fluorescence and ROS-scavenging systems to salt stress during seedling and reproductive stages in rice. Annals of botany, 99(6), 1161-1173. https://doi.org/10.1093/aob/mcm052
31. Mostofa, M. G., Seraj, Z. I., & Fujita, M. (2014). Exogenous sodium nitroprusside and glutathione alleviate copper toxicity by reducing copper uptake and oxidative damage in rice (Oryza sativa L.) seedlings. Protoplasma, 251, 1373-1386.
32. Mostofa, M. G., Hossain, M. A., & Fujita, M. (2015). Trehalose pretreatment induces salt tolerance in rice (Oryza sativa L.) seedlings: oxidative damage and co-induction of antioxidant defense and glyoxalase systems. Protoplasma, 252, 461-475. https://doi.org/10.1007/s00709-014-0691-3
33. Muthuramalingam, P., Jeyasri, R., Rakkammal, K., Satish, L., Shamili, S., Karthikeyan, A., … & Ramesh, M. (2022). Multi-Omics and Integrative Approach towards Understanding Salinity Tolerance in Rice: A Review. Biology, 11(7), 1022. https://doi.org/10.3390/biology11071022
34. Nagarajan, S., Varatharajan, N., &Gandhimeyyan, R. V. (2022). Understanding the responses, mechanism and development of salinity stress tolerant cultivars in Rice. Integrative advances in rice research, 91. DOI: 10.5772/intechopen.99233
35. Nedjimi, B. (2017). Calcium application enhances plant salt tolerance: a review. Essential Plant Nutrients: Uptake, Use Efficiency, and Management, 367-377. https://doi.org/10.1007/978-3-319-58841-4_15
36. Noreen, S., Sultan, M., Akhter, M. S., Shah, K. H., Ummara, U., Manzoor, H., … & Ahmad, P. (2021). Foliar fertigation of ascorbic acid and zinc improves growth, antioxidant enzyme activity and harvest index in barley (Hordeumvulgare L.) grown under salt stress. *Plant Physiology and Biochemistry*, 158, 244-254. https://doi.org/10.1016/j.plaphy.2020.11.007
37. Patakas, A., Nikolaou, N., Zioziou, E., Radoglou, K. &Noitsakis, B. (2002). The role of organic solute and ion accumulation in osmotic adjustment in drought-stressed grapevines. *Plant Science,* 163(2), 361-367. https://doi.org/10.1016/S0168-9452(02)00140-1
38. Pharmawati, M. &Wijaya, I. M. A. S. (2019). Changes in growth, biochemical components and antioxidant genes expression in rice seedling (Oryza sativa L.) cultivar 'IR64'under salt stress. *Indian Journal of Agricultural Research,* 53(4), 478-482. DOI: 10.18805/IJARe.A-399
39. Qin, H., Li, Y., & Huang, R. (2020). Advances and challenges in the breeding of salt-tolerant rice. *International Journal of Molecular Sciences,* 21(21), 8385. https://doi.org/10.3390/ijms21218385
40. Rahman, A., Nahar, K., Hasanuzzaman, M. & Fujita, M. (2016). Calcium supplementation improves Na+/K+ ratio, antioxidant defense and glyoxalase systems in salt-stressed rice seedlings. *Frontiers in Plant Science,* 7, 609. https://doi.org/10.3389/fpls.2016.00609
41. Raja, V., Wani, U. M., Wani, Z. A., Jan, N., Kottakota, C., Reddy, M. K., ... & John, R. (2022). Pyramiding ascorbate–glutathione pathway in Lycopersicumesculentum

confers tolerance to drought and salinity stress. *Plant Cell Reports*, 41(3), 619-637. https://doi.org/10.1007/s00299-021-02764-8

42. Rajput, V. D., Harish, Singh, R. K., Verma, K. K., Sharma, L., Quiroz-Figueroa, F. R., ... & Mandzhieva, S. (2021). Recent developments in enzymatic antioxidant defence mechanism in plants with special reference to abiotic stress. *Biology,* 10(4), 267. https://doi.org/10.3390/biology10040267
43. Rezvi, H. U. A., Tahjib□Ul□Arif, M., Azim, M. A., Tumpa, T. A., Tipu, M. M. H., Najnine, F., ... & Brestič, M. (2023). Rice and food security: Climate change implications and the future prospects for nutritional security. *Food and Energy Security,* 12(1), e430. https://doi.org/10.1002/fes3.430
44. Riyazuddin, R., Verma, R., Singh, K., Nisha, N., Keisham, M., Bhati, K. K., ... & Gupta, R. (2020). Ethylene: A master regulator of salinity stress tolerance in plants. Biomolecules, 10(6), 959. https://doi.org/10.3390/biom10060959
45. Safdar, H., Amin, A., Shafiq, Y., Ali, A., Yasin, R., Shoukat, A. & Sarwar, M. I. (2019). A review: Impact of salinity on plant growth. *Nat. Sci.,*17(1), 34-40.
46. Sampangi-Ramaiah, M. H., Dey, P., Jambagi, S., VasanthaKumari, M. M., Oelmüller, R., Nataraja, K. N., ... & Uma Shaanker, R. (2020). An endophyte from salt-adapted Pokkali rice confers salt-tolerance to a salt-sensitive rice variety and targets a unique pattern of genes in its new host. *Scientific Reports,* 10(1), 1-14. https://doi.org/10.1038/s41598-020-59998-x
47. Shahid, S. A., Abdelfattah, M. A., Wilson, M. A., Kelley, J. A, & Chiaretti, J. V. (2014). United Arab Emirates keys to soil taxonomy (p. 108). New York, NY, USA: Springer.
48. Singha, S. & Choudhuri, M. A. (1990). Effect of salinity (NaCl) stress on H2O2 metabolism in Vigna and Oryza seedlings. *Biochemie und Physiologie der Pflanzen*, 186 (1), 69-74. https://doi.org/10.1016/S0015-3796(11)80295-7
49. Muthayya, S., Sugimoto, J. D., Montgomery, S. & Maberly, G. F. (2014). An overview of global rice production, supply, trade, and consumption. *Annals of the new york Academy of Sciences,* 1324(1), 7-14.
50. Yadav, S., Irfan, M., Ahmad, A., & Hayat, S. (2011). Causes of salinity and plant manifestations to salt stress: a review. *Journal of Environmental Biology*, 32(5), 667.
51. Yang, H., Shukla, M. K. & Du, T. (2023). Assessment of plant mineral nutrition concentrations of tomato irrigated with brackish water and RO concentrate. *Journal of Plant Nutrition*, 1-18.
52. Yi, Y., Peng, Y., Song, T., Lu, S., Teng, Z., Zheng, Q., ... & Ye, N. (2022). NLP2-NR module associated NO is involved in regulating seed germination in rice under salt stress. *Plants,* 11(6), 795. https://doi.org/10.3390/plants11060795