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**Review Article**

# The critical role of nitrogen in plants facing the salinity stress: Review and future prospective

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## Abstract

Salinity stress is a serious abiotic stress that negatively affect the crop growth and development. Mineral nutrient supplementation is considered as an effective strategy to mitigate the adverse effects of salinity. Nitrogen (N) is an important nutrient needed for plants and its application also an effective strategy to mitigate adverse impacts of salinity. Salinity stress disturbs plant physiological, and biochemical functions, antioxidant activities, cellular membranes, antioxidant activities and nutrient uptake thereby cause significant reduction in plant growth and development. The application of N maintains membrane stability, plant water relations, leaf gas exchange characteristics, and protect the plants from oxidative damages which induce the salt tolerance in plants. Besides, this N also improves nutrient uptake and it also induce cellular signaling that mitigate the adverse impacts of salinity. Therefore, it is interesting to understand the role of N in inducing salt tolerance in plants. In present review the mechanisms of N uptake and assimilation in plants under saline conditions are discussed. The present review provides information on how N mitigates ionic toxicity, and oxidative damages and maintains nutrient balance to counter the toxic effects of salinity stress in plants. This review will help the readers to learning more about the role of N in inducing salt tolerance in plants.

***Keywords:*** antioxidants; ionic toxicity; nitrogen; oxidative damage; salinity

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## Introduction

The increasing soil salinization became a global threat to crop production and more than half of the arable land by would be the salt affected lands by the end of 2050 (Qureshi and Daba, 2020; Naz *et al.*, 2022; Nazir *et al.*, 2023). The increasing salinization in agricultural land significantly depleting the nitrogen status and it is predicted that the soil fertility status will reduce up to 50% in middle of 21st century (Aslam *et al.*, 2017). Soil salinization is foremost noxious among all other abiotic stresses affects plant growth, yield and grain quality indices (Chaudhry and Sidhu, 2022). Seed germination is imperative stage significantly affected with reduced water imbibition due to less soil osmotic potential in saline soil (Debez *et al.*, 2020; Lokupitiya *et al.*, 2020; Mwando *et al.*, 2020; Krichen *et al.*, 2023). Salinity caused ion toxicity in embryo that alters the protein metabolism, decreased the adenosine triphosphate (ATP) generation and hormonal regulation that significantly reduced the germination percentage of a crop in salt affected soils (Bilkis *et al.*, 2016; El-Hendawy *et al.*, 2019; Bagwasi *et al.*, 2020). Salinity induced osmotic stress decreased the water intake, root and shoot cell expansion, stomatal conductance, and $CO_2$ assimilation (Fricke *et al.*, 2004; Wegner *et al.*, 2011; Shabala *et al.*, 2016; Alkharabsheh *et al.*, 2021; Hasanuzzaman *et al.*, 2023).

Further, the photosynthetic machinery of a plant greatly affected by sodium toxicity (Al-shareef and Tester, 2019; Parkash and Singh, 2020; Talaat *et al.*, 2023). The increased sodium accumulation reduced the $\alpha$-amylase activity responsible for protein and starch synthesis, ATP breakdown and Calvin cycle, consequently growth decreases (Benito *et al.*, 2014; Wu *et al.*, 2018). Many researchers reported relative water content (RWC) as effective indicator of salinity tolerance helps maintain turgidity in plants (Saeed *et al.*, 2019), whereas RWC were decreased up to 6.7% in salt sensitive wheat variety compared to 3.5% reduction of RWC in tolerant genotype (Nassar *et al.*, 2020). Moreover, the membrane integrity remarkably decreased under salt stress (Senadheera *et al.*, 2012; Saddiq *et al.*, 2021). Salinity triggers the reactive oxygen species (ROS) (e.g., MDA, $H_2O_2$) production and damages the cell membranes whereas lipid peroxidation disturbs chlorophyll synthesis caused a significant reduction in transpiration and photosynthesis (Abbasi *et al.*, 2016; Kamran *et al.*, 2020; Singh *et al.*, 2013; Rangani *et al.*, 2016) (Table 1). In addition, the rubisco enzyme activity reduced under salinity stress which led to less PS-II efficiency subsequently less biomass and yield produced (Abrar *et al.*, 2020).

Further, plant growth, developmental processes and yield significantly affected by salt stress however, the extent depends upon growth stage of cultivar and duration of salinity (Al-shareef and Tester, 2019; Ijaz *et al.*, 2022). The yield of salt sensitive wheat cultivar decreased up to 67% at 120 mM salinity level (Alkharabsheh *et al.*, 2021). For instance, grain number, test weight and rice yield were reduced at 4 dS $m^{-1}$ (Thitisaksakul *et al.*, 2015). Infertile pollen production followed by pollen abortion are common under salinity stress that significantly reduced 36% rice yield (Al-Ashkar *et al.*, 2019, Kongpun *et al.*, 2020). Further, salt toxicity also deteriorates the grain quality (starch and amylase) indices of a crop (Li *et al.*, 2019). Similarly, less carbohydrate and protein contents in wheat, maize, and barley grains were reported from saline soils (Jamshidi and Javanmard, 2018; Li *et al.*, 2019).

Along with deteriorating the crop traits, salinity induces disturbance in soil health and fertility status (Maurya *et al.*, 2020). Better soil quality with improved fertility status is the competence to augment crop productivity in agricultural production system (Maurya *et al.*, 2020) whereas deposition of dissolved salts brings soil under salinization, which significantly reduce the soil productivity (de Souza Silva and Fay, 2012; Amini *et al.*, 2016). Salinization decreases the microbial population that destroy the soil structure (Feng *et al.*, 2023). Salt stress imbalance the soil nutrition and induces less water infiltration rate; organic carbon (%) and low C:N ratio that decrease the soil fertility status and therefore, crop productivity reduces (Haj-Amor *et al.*, 2022).

Nitrogen is imperative macro-nutrient determines the soil fertility status necessary to enhance crop production (Zhang *et al*., 2021). Generally, nitrogen fertilization boosts the crop vegetative growth that increase the crop biomass and yield (Kubar *et al*., 2022; Mahboob *et al*., 2023). Optimum nitrogen fertilization increased the soil water retention percentage, improve soil structure, nitrogen uptake and nitrogen use efficiency that augments the crop yield (Gao *et al*., 2015; Mustafa *et al*., 2022; Liu *et al*., 2023). While, increased application of nitrogenous fertilizer enhances the production cost and reduce the net benefit ratio (Euclides *et al*., 2022). However, soil salinity remarkably reduces the nitrogen uptake efficiency and increase the nitrogen losses in environment (Dubey *et al*., 2021).

The excess $Cl^-$ ion in saline soil compete with nitrate ($NO_3^-$) to develop ion imbalance and ion toxicity, thus effects nitrification and ammonification processes and reduced nitrogen uptake, transport and assimilation in plants (Campbell, 1999; Zhao *et al*., 2020; Liu *et al*., 2022; Tzortzakis *et al*., 2022). The reduced nitrogen uptake of many field crops observed in saline stressed soils (Dalio *et al*., 2013; Singh *et al*., 2016; Shahzad *et al*., 2017; Fuertes-Mendizábal *et al*., 2020). In addition, salinity reduced the nitrate reductase (NR) activity in water stressed condition, consequently plant produce less assimilates (Ashfaque *et al*., 2014; Shao *et al*., 2015; Singh *et al*., 2016; Rohilla and Yadav, 2023). Researchers also reported nitrogen to facilitate in defensive mechanisms, improves physiological and metabolic responses under salinity stress (Krapp, 2015; Zhang *et al*., 2020a; Zhang *et al*., 2020b; Nazir *et al*., 2023). Therefore, a comprehensive understanding on nitrogen nutrition is effective to enhance crop productivity in salt-affected soil. For this, nitrogen dynamics in soil and plants under salinity stress is still need to disclose for enhancing crop production challenges. The present review is a little contribution towards fate of nitrogen in salt-affected soil and plants. Comprehensive research on aforesaid big agricultural problem will also provide valuable insights of salinity stress tolerance of plants.

## Causes of salinity

Salts accumulate in groundwater and soil over an extended period leads to natural process of primary salinity development. Naturally, two natural processes; weathering of the parent material, and wind- and rain-born sea salt (NaCl) deposition increases salinization (Munns, 2009). On contrary, the human-induced (secondary salinity) activities include: fallowing of land, salt-affected water use for irrigation (saline water leaves salts on soil surface after evaporation), poor drainage, seepage from canals, improper slope, over irrigation and intensive rice cultivation in low water table areas, also increased the salinized area in the world (Siyal *et al*., 2002; Khan and Abdullah, 2003; Munns, 2009).

## Extent of salt stress

The estimation of salinity affected area is pivotal to address the most prevailed challenges to agriculture. Soil salinization is continuously soaring up with various anthropogenic activities. The extent of salinity stress has increased up to 397 million ha from 1970-1980 (Negacz *et al.,* 2022). Ghassemi et al. (1995) reported 20% of irrigated land comes under salinity. Moreover, Wicke *et al. (*2011) reported 840 million hectares area is under salt stress and they further classified it in saline (683 million ha) and sodic (157 million ha) soils. Recently, the estimated area under salinity reached up to 6.5 billion ha from 14 billion ha of the total agriculture land comes under semi-arid and arid regions. From these, 1 billion ha land is salt affected (Qadir al., 2014; Mohamed *et al.,* 2019). The recent report on land mapping (73% so far) stated that 424 million ha land of top most soil (0-30 cm) and 833-million-hectare of sub soil (30-100 cm) comes under salt stress (FAO, 2021). Additionally, Negacz (2022) reported the salinity stress exposed to 85% of top soil and 62% of sub-soil of arable lands. The continuous increasing of salinity stress is the foremost indicator of doing a comprehensive research work on improving salinity stress to cope the future challenges.

## Plant responses to salinity stress

Seed germination is sensitive to salt stress where the soil osmotic potential and water uptake decreased (Debez *et al*., 2020; Lokupitiya *et al*., 2020; Mwando *et al*., 2020). Under salinity, $Na^+$ and $Cl^-$ toxicity disturbs the hormonal and enzymatic (α-amylase) activities and protein synthesis subsequently less sugar translocation to growing embryo in seed that delays germination (Bilkis *et al*., 2016; El-Hendawy *et al*., 2019; Debez *et al*., 2020; Bagwasi *et al*., 2022). Further, salt stress also reduced the plant growth and developmental stages, however, the extent of reduction varies with plant species, growth stage, intensity and duration of salinity stress (Al-shareef and Tester, 2019). Plants under saline environment experienced less water intake owing to osmotic stress reduced the cell expansion and stomatal closure (Figure 1). Thus, plant growth decreased in few minutes (Shabala *et al*., 2016; Nawaz *et al*., 2022). Moreover, the $CO_2$ assimilation, protein synthesis, assimilate partitioning through various metabolic pathways reduced under salinity stress (Al-shareef and Tester, 2019; Parkash and Singh, 2020). In second phase, the high salinity stress brings $Na^+$ accumulation decreased the enzyme activity, protein and starch synthesis, glycolysis, polyamine and phenylpropanoid pathways, which disturbs the Calvin cycle efficiency and causes a significant decrease in plant growth (Benito *et al*., 2014; Wu *et al*., 2018).

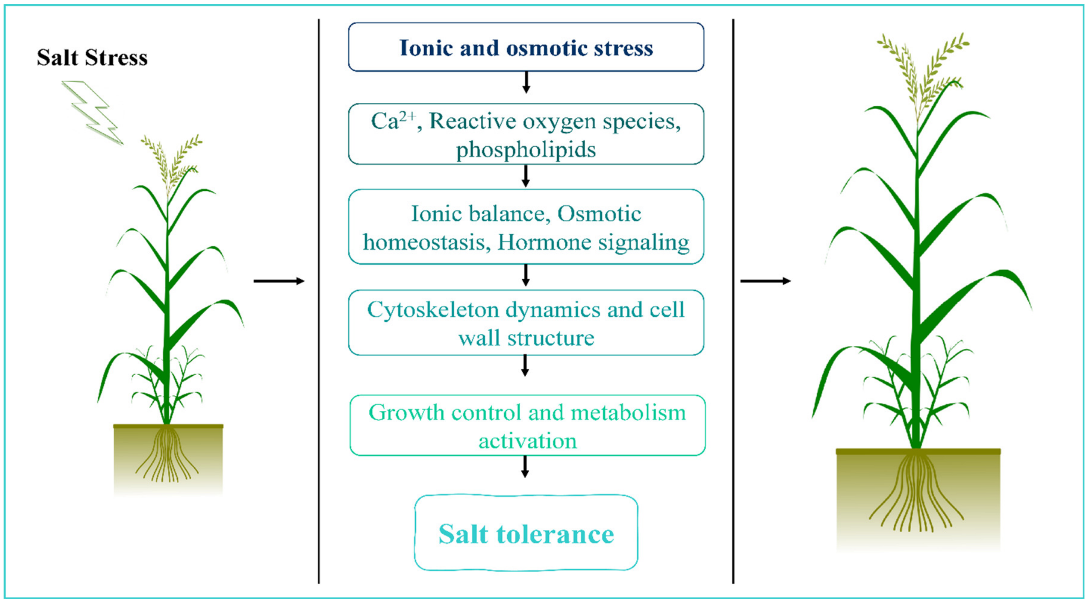

**Figure 1.** Plant salt stress response: Salinity causes ionic and osmotic stress whereas plants increase $Ca^{2+}$ and ROS signaling, and phospholipid composition after sensing $Na^+$ and hyperosmolality. These signals induce phytohormone signaling to maintain ion balance and osmotic homeostasis to reduce salt stress

However, the genotypes vary greatly in response to salinity stress (120 mM) and highest yield reduction (67%) was observed in sensitive genotype compared to salt-tolerant (41% yield reduction) variety of wheat crop (Alkharabsheh *et al*., 2021). Relative water contents (RWC) are imperative to consider the salt tolerance ability of a genotype (Saeed *et al*., 2019). Researchers found 47.76% higher RWC in salt tolerant cultivars compared to salt sensitive cultivars of wheat (Nassar *et al*., 2020). Further, the membrane integrity damages under salt toxicity and increase the loss of essential cellular substances affecting plant growth (Nawaz *et al*., 2022) (Figure 2). The ROS, MDA contents and lipid peroxidation increases under salt stress (Abbasi *et al*., 2016). Chlorophyll contents are imperative to increase photosynthetic efficiency whereas the chlorophyll contents and photosynthetic apparatus disturbs by ROS and MDA contents under salt stress (Rangani *et al*., 2016;

Kamran *et al.*, 2020). Salt stress triggers early leaf senescence and reduce the leaf area, stomatal conductance, PS-II efficiency led to less biomass production (Abrar *et al.*, 2020).

**Table 1.** Effects of salt stress on growth, physiological, biochemical and yield attributes of crops

| Crops | Salt stress | Effects | References |
|---|---|---|---|
| Barley | 100 mM NaCl | Salt stress significantly reduced the plant height, spike length, grains/spike, grain yield, $K^+$ and relative water contents decreased whereas, the ELR, POD, and $Na^+$ contents were increased in plant leaves under salinity stress | Elsawy *et al.*, 2022 |
| Sugar Beet | 9.28 dS $m^{-1}$ NaCl | Salinity stress reduced the leaf area, damage cell membrane stability and sugar production by reducing the anti-oxidant activity under increased $Na^+$, total phenolic and flavonoid contents. | El-Mageed *et al.*, 2022 |
| Pea | 150 mM NaCl Hoagland solution | Salt stress drastically decreased the shoot and root length, shoot weight (fresh and dry weight), $CO_2$ intake, transpiration, stomatal conductance and WUE in plants. Additionally, the yield attributes (number of pods, pods weight decreased) were reduced due to increased uptake of $Na^+$ ions and free proline content production. | Shahid *et al.*, 2022 |
| Quinoa | 300 mM NaCl | The growth parameters (stem and root elongation, seeds dry weight) along with stomatal conductance and photosynthetic efficiency reduced under salt stress. While, the increased production of MDA, $H_2O_2$ content and antioxidant enzymes were observed in leaves | Salma *et al.*, 2023 |
| Cowpea | 8000 ppm NaCl | Salinity stress decreased plant height, fresh weight of shoots, and photosynthetic pigments that reduced the yield. Whereas, higher proline contents were observed in leaves. | El-Taher *et al.*, 2022 |
| Chickpea | NaCl level 150 mM | The root and shoot length; chlorophyll and carotenoid contents in chickpea were reduced in salt affected soils. Whereas, proline contents were amplified with significant reduction in yield under salt stress. | Mushtaq *et al.*, 2021 |
| Rice | 200 mM NaCl | Less water imbibition under NaCl stress led to the osmotic and ionic imbalance, decreased germination (%) and damage to cellular membrane. Under salinity, $Na^+$ accumulation, MDA, and $H_2O_2$ contents were increased that reduced the rice production. | Alshiekheid *et al.*, 2023 |
| French Bean | 100 mM NaCl | In salt affected soils, plants absorbed higher $Na^+$ ions that reduced the growth parameters (root/shoot length, leaf area, and plant fresh/dry weight), MSI, RWC, chlorophyll contents and final yield of crop. | Youssef *et al.*, 2023 |
| Lentil | 100 mM NaCl | Salinity caused considerable damage to lentil crop by reducing the growth parameters, RWC, chlorophyll contents, with increased MDA, $H_2O_2$, SOD, CAT, and POD biosynthesis. | Yasir *et al.*, 2021 |
| Maize | 100 of 1 M NaCl hogland solution | Salt stress reduced root and shoot length due to higher $Na^+$ ions that reduced the photosynthetic pigments resulting in significantly reduction in maize yield. | Zahra *et al.*, 2020 |

$Na^+$, sodium; $K^+$, potassium; SOD, Superoxide dismutase; POD, Peroxidase; CAT, Catalase, ELR, Electrolyte leakage, WUE, Water use efficiency; $CO_2$, Carbon dioxide; MDA, Malondialdehyde; $H_2O_2$, Hydrogen peroxide; MSI, Membrane stability index; RWC, Relative water contents

Moreover, the nutrient availability; uptake efficiency and nutrient homeostasis significantly reduced in plants under salinity stress. Less water potential in soil lowers the plant growth whereas the antagonistic effect of $Na^+$ accumulated in plants suppresses the uptake of nutrients (N, P, K, Ca, Mg,$NO_3^-$, $NH_4^+$ etc) (Hussain *et al.*, 2015). Amongst these, nitrogen found imperative for plant growth, development and yield whereas, the nitrogen nutrition affects under salinity stress (Jahan *et al.*, 2021). The specific nitrogen compounds (e.g., proline, glutamine and asparagine) are responsible for nitrogen uptake decreases therefore, less nitrogen uptake observed under salinity stress (Ashraf *et al.*, 2018).

## Nitrogen uptake in saline environment

The presence of salt ions restricts $NO_3^-$ and $NH_4^+$ uptake, disturb the N loading in xylem (root) causes nitrogen deficiency in plants (Abd-El-Baki *et al.*, 2000; Parida and Das, 2004). These salts develop osmotic imbalance and damage the root membrane structure (Gessler *et al.*, 2005; Debouba *et al.*, 2007) that affect the photosynthesis and reduce crop growth under saline conditions (Ullrich, 2001). In salinity, $Cl^-$ compete with $NO_3^-$ ions, reduce nitrogen intake and translocation in plants (Abdelgadir *et al.*, 2005). Therefore, nitrogen uptake decreases under salinity stress (Tabatabaei, 2006; Chen *et al.*, 2007; Hutsch *et al.*, 2016; Annunziata *et al.*, 2017). The source of chloride ions has key importance to its role towards inhibiting the nitrate contents. Interestingly, $Cl^-$ ion from $CaCl_2$ perform inhibitory role compared to $Cl^-$ comes from KCl (Kafkafi *et al.*, 1992). Whereas, KCl inhibit $NO_3^-$ contents only under high salinity (100–200 mol $m^{-3}$). Though, the influence of NaCl and KCl found similar, the $NO_3^-$ inhibition was prominent at low salinity in presence of Ca2C (Kafkafi *et al.*, 1992). In addition, the antagonistic effect of NaCl was observed for $NH_4^+$ uptake under salinity stress (Camberato and Bock, 1989; Bradley and Morris, 1991; Hawkins and Lewis, 1993; Dluzniewska *et al.*, 2007; Bahmanzadegan and Aboutalebi, 2013; Dai *et al.*, 2015). Furthermore, less water availability disturbs soil-water potential, caused osmotic stress that reduced the nitrogen uptake under salinity stress (Lea-Cox and Syvertsen, 1993; Grattan and Grieve, 1998; da Silveira *et al.*, 1999; Halperin *et al.*, 2003; Abdelgadir *et al.*, 2005; Ehlting *et al.*, 2007; Zakery-Asl *et al.*, 2014). Further, the nitrate dependent transporting system permits the $Na^+$ loading in xylem, therefore, high $Na^+$ accumulates in plants (Álvarez-Aragón and Rodríguez-Navarro, 2017) consequently the $NO_3^-$ flow rate in soil and plant-nitrogen uptake hinders that reduce the protein metabolism, cell development and crop yield (Raddatz *et al.*, 2020; Yu *et al.*, 2023; Nazir *et al.*, 2023; Doncato and Costa, 2023).

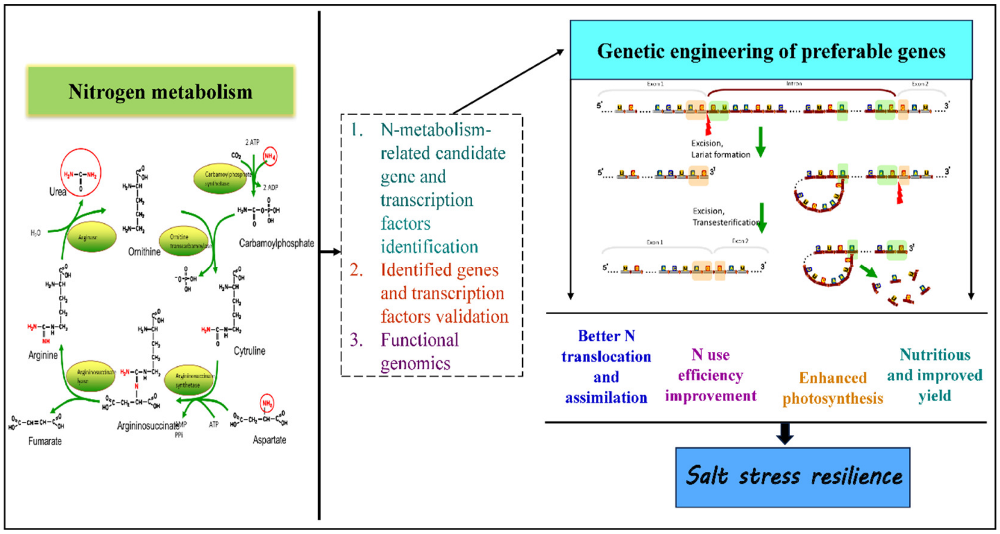

**Figure 2.** Genetically modified nitrogen targets. Overexpression of nitrate and ammonium transporter genes and transcription factors improves NUE, photosynthetic efficiency, crop productivity, nitrate and ammonium intake, and salt-stress resistance.

## Nitrogen assimilation in plants under saline conditions

The nitrogen assimilation is imperative for plant growth, development and functioning particularly under abiotic stress conditions (Lea and Mifflin, 2003). Plants used nitrogen assimilates to respond ROS produced in abiotic stresses by osmotic adjustment and adopting scavenging mechanism (Gimeno *et al.*, 2009). Mostly plant uptake nitrogen in form of $NH_4$ that causes proton extrusion, alter the cytosolic pH and disconnect the photophosphorylation processes in plant cells. Therefore, rapid conversion of $NH_4$ into organic N molecules is necessary to prevent $NH_4$ toxicity within the plant body. Firstly, plants reduce the $NH_4$ into inorganic molecular nitrogen, and later used NR and NiR to produce organic form of nitrogen (Zhang *et al.*, 2014). This phenomenon involves GS/GOGAT pathway where GS produces glutamine (Gln) from $NH_4$ that is converted into glutamate (Glu) with the involvement of 2-oxoglutarate in GOGAT pathway (Lancien *et al.*, 2000). Salinity stress restrict the nitrogen ($NH_4/NO_3^-$) assimilation and reduce the plant nitrogen contents (Hoai *et al.*, 2005) (Table 2). Plants produced different nitrogen-based compounds (protein, amines, A.A.) under stress however, a significant detrimental effect of salinity stress exposed in salt sensitive plant species compared to salt tolerant varieties (Yu *et al.*, 2015). Thus, salt stress hampered the nitrogen uptake, transportation whereas the $NO_3^-$ reduction and $NH_4^+$ assimilation significantly reduced by the inactivation of nitrate assimilating enzymes, subsequently, less plant growth observed under stress conditions (Yu *et al.*, 2016; Tian *et al.*, 2022; Nanda *et al.*, 2022).

### *$NO_3^-$ reduction in saline environment*

Nitrate ($NO_3^-$) form is the prime importance to meet plant nitrogen demand and $NO_3^-$ assimilation provides 99% organic nitrogen in biosphere (Yao *et al.*, 2008). Plant store nitrate ($NO_3^-$) in root cells (vacuole) whereas its reduction takes place in cytoplasm prior to transport in leaves (Crawford, 1995). The $NO_3^-$ reduction involves assimilatory pathway comprising two steps (Cao *et al.*, 2008); NR- a cytoplasmic enzyme use pyridine nucleotide that reduces the $NO_3^-$ into $NO_2^-$ that is highly reactive therefore plant cell immediately transports the $NO_2^-$ form cytosol to chloroplast in leaves and plastids in roots where $NO_3^-$ reduction in $NH_4^+$ completed using NiR (Rosales *et al.*, 2011). This reduced $NH_4^+$ is then enter in GS/GOGAT pathway and assimilated into amino acids (Hirel and Lea, 2002). $NO_3^-$ assimilation is sensitive in salinity stress decreases N uptake, transportation and $NO_3^-$ reduction (Maaroufi-Dguimi *et al.*, 2011; Queiroz *et al.*, 2012). Salt sensitive cultivars translocate high $NO_3^-$ contents in roots caused $NO_3^-$ deficiency in shoot that stop the signaling of NR for protein synthesis thus plant growth decreased under salinity (Debouba *et al.*, 2007). Moreover, decreased protein metabolism and AA synthesis observed due to less N uptake and $NO_3^-$ transportation under salinity stress (Hossain *et al.*, 2012; Ahanger and Agarwal, 2017). Salt stress decreased the enzyme synthesis and stop the NR activity responsible for $NO_3^-$ assimilation (Ahanger and Agarwal, 2017). Furthermore, less nitrogen assimilation is due to reduced $NO_3^-$ uptake under salt stress compared to $NO_3^-$ reduction in plants (Hossain *et al.*, 2012). The efficiency of nitrate transporters decreased in saline soils that reduced the $NO_3^-$ uptake (Hossain *et al.*, 2012). Thus, the salinity injury to $NO_3^-$ transporter is crucial rather to less $NO_3^-$ reduction for plants under salinity stress (Figure 2). In saline conditions, less NR activity observed in leaves that reduced the $NO_3^-$ assimilation (Parida and Das, 2004) whereas non-significant effect of root NR activity reported under salinity stress (Meloni *et al.*, 2004). The decreased NR activity in leaves could be attributed to less transportation of $NO_3^-$ from root to shoot through xylem or vacuole to cytoplasm (Maighany and Ebrahimzadeh, 2004). In addition, the activity of amino acids; asparagine (Asn), glutamate (Glu), aspartate (Asp) and glutamine (Gln) responsible for nitrogen transportation significantly reduced under saline environment (Shahzad *et al.*, 2017; Fuertes-Mendizábal *et al.*, 2020). Thus, the salinity found detrimental for uptake, $NO_3^-$ reduction and nitrogen metabolism in plants (Chakraborty *et al.*, 2018; Isayenkov and Maathuis, 2019; Huang *et al.*, 2020; Yin *et al.*, 2022).

### *$NH_4^+$ assimilation in saline environment*

Plant growth increased with the availability of reduced nitrogen since it is necessary for synthesizing different cellular components such as amino acids. Therefore, inorganic N is converted to ammonium ions ($NH_4^+$) through a dual-enzymatic pathway involving first using GS-catalyzed synthesis of glutamine from ammonia before converting it to glutamate with GOGAT enzyme activity that completes nitrogen assimilation (Ruiz *et al.*, 2007). Glutamine synthetase (GS) catalyzed the production of glutamine, which is then converted to glutamate-by-glutamate synthase (GOGAT), in two-step conversion of inorganic N to $NH_4^+$ ions. The assimilation of $NH_4^+$ into organic N compounds is possible either thorough direct absorption, nitrate reductase (NR) activity, photorespiration, dinitrogen fixation, or by deamination of nitrogenous compounds. However, GS and GOGAT enzymes plays a significant role in $NH_4^+$ assimilation (Frechilla *et al.*, 2002; Esposito *et al.*, 2005; Wickert *et al.*, 2007). Numerous studies reported $NH_4^+$ assimilation in salt stress varies amongst the cultivars and soil characteristics under salinity (da Silveira *et al.*, 2003; Debouba *et al.*, 2006; Queiroz *et al.*, 2012; Yu *et al.*, 2015). Salinity caused $NO_3^-$ deficiency and resulted in downregulation of genes (OsGS1; 2, OsGS2, OsNR1, and OsFd-GOGAT) involved in $NH_4^+$ assimilation under salt stress (Wang *et al.*, 2012). Increased activity of GS than GOGAT observed under normal conditions while both are responsible for $NH_4^+$ assimilation (Meng *et al.*, 2016). The enzyme (GS) and GOGAT sensitive under salinity that decreased their activities however the enzymatic (GS) activity is limiting factor for $NH_4^+$ assimilation in saline stress (Meng *et al.*, 2016). Moreover, salt reduced the activity of NADH-GOGAT that also lowers the $NH_4^+$ assimilation in plants (Kawakami *et al.*, 2013).

**Table 2.** Effects of salinity on N-transporters and metabolizing enzymes involve in nitrogen assimilation in plants

| Species | Salt stress | Effects | References |
|---|---|---|---|
| *Simon poplar* | 75 mM NaCl | The activity of NR, NiR, GS and GOGAT was significantly reduced and consequently less nitrogen assimilation observed under salinity stress. | Meng *et al.*, 2016 |
| Peanut | 200 mM NaCl | Salt stress suppressed the expression of $NO_3^-$ transporter that decrease the nitrogen metabolism in plant. | Zhang *et al.*, 2020 |
| Barley | 150 mM NaCl | Salt stress reduced the activity of APX, Fd-GOGAT and Plastidic P2-G6PDH activity that decrease nitrate assimilation in plants. | Ben Azaiez *et al.*, 2020 |
| Tomato | 300 mM NaCl | The concentration of $NO_3^-$ was dramatically reduced under salinity which led to a reduction in NR and GS activity, therefore, nitrogen assimilation reduced. | Abouelsaad *et al.*, 2016 |
| Grey poplar | 75 mM NaCl | Nitrogen uptake and assimilation was reduced due to decrease in NR activity in alt affected soil. | Ehlting *et al.*, 2007 |
| Wheat | 200 Mm NaCl | A noticeable reduction in nitrogen metabolism due to less efficiency of NR and GOGAT under NaCl stress while, the activity of AlaAT, AsAT, and GDH was stimulated at higher salinity level. | Ahanger *et al.*, 2017 |
| Mustard | 100 mM NaCl | Salinity decreased NR activity whereas the GK and P5CS activity increased causes a significant reduction in the nitrogen assimilation in plants | Iqbal *et al.*, 2015 |
| *Achnatherum Inebrians* | 400 Mm Nacl | A significant decline in NR, NiR and GS activity under salt stress caused to reduction in nitrogen assimilation in plants | Wang *et al.*, 2019 |
| Soyabean | 10 dS $m^{-1}$ NaCl | Salt stress reduced the activity of GDH, GS, GOGAT, and NR enzymes responsible for nitrogen assimilation and metabolism, therefore, less N assimilation found in salt affected plants. | Farhangi-Abriz *et al.*, 2018 |
| Rice | 150 mM NaCl | The activity of GDH GS, GOGAT, and NR decreased by salt stress that reduced the nitrogen metabolism in plants. | Teh *et al.*, 2016. |

| | | | |
|---|---|---|---|
| Sweet potato | 100 mM NaCl for 6 days | NaCl induced $NH_4^+$ efflux depleted cellular pool of $NH_4^+$ that disrupt the $NH_4^+$ assimilation by a significant reduction in the GS and NADH-GOGAT activities in root (50% and 40%) and leaves (40% and 60%) | Yu *et al.*, 2015 |

NR, Nitrate reductase; NiR, Nitrite reductase; GS, Glutamine synthetase; GOGAT, Glutamine oxoglutarate aminotransferase; APX, Ascorbate peroxidase; Fd-GOGAT, Ferredoxin-dependent glutamate synthase; GDH, Glutamate dehydrogenase; GK, γ-glutamyl kinase

Glutamine (Glu) and amino acid (AA) production increases by plants under normal conditions for $NH^{4+}$ assimilation using GS/GOGAT pathway whereas salt stress decreases the Glu and AA synthesis to restrict GS/GOGAT pathway, in response, GDP pathway activates in plants for $NH_4^+$ assimilation under saline conditions. The similar mechanism was observed by various researchers in common bean, rice, wheat and tomato growing under saline conditions (Khadri *et al.*, 2001; Wei *et al.*, 2004; Kwinta and Cal, 2005; Zhang *et al.*, 2014). Kumar *et al.* (2000) observed the breakdown of glutamic acid into 2-oxoglutarate and deaminating activity of GDH pathway in which enzymes sustained the carbohydrate metabolism by supplying an intermediate to tricarboxylic acid (TCA) cycle in rice under salinity stress. Energy ($NAD^+$) produces during GDH pathway used to regulate various metabolic functions (Lasa *et al.*, 2002).

On the other hand, high concentration of $NH_3$ and free amino acids produces by catabolic reactions of protein in leaf under salinity stress. It includes following methods: detoxifying excess $NH_3$ through GS/GOGAT pathway, and supplementing the normal pathway by additional $NH_3$ utilizing reactions, initiated only at times when there is an excessive level of $NH_3$ in tissues (GDH pathway) (Wang *et al.*, 2012). Both of these mechanisms seem to be operative during certain environmental conditions with the "additional $NH_3$ utilizing reactions" which are particularly important during accumulation of the N-containing compounds (Rabe 1994). It is summarized that salinity stress could result in elevated levels of $NH_3$ either due to inhibition of $NH_4$ assimilation or enhanced proteolysis. The accumulation of $NH_3$ is paralleled by a sharp rise in GDH activity, which is primarily involved in the catabolism of glutamate to oxoglutarate, thus providing carbon skeleton for tricarboxylic acid (TCA) cycle, with the concomitant release of $NH_3$. The excess of NaCl and $Cl^-$ might change the pathway of $NH_4$-C assimilation by inactivation of GS/GOGAT pathway and stimulation of GDH pathway.

## Effects of different forms of nitrogen on salinity tolerance

The form of nitrogen determines the plant response to salinity stress (Crawford and Forde, 2002). Generally, plant uptake nitrogen either $NH_4^+$ or $NO_3^-$ ion (Zhonghua *et al.*, 2011). Plants become more sensitive to salt in presence of $NH_4^+$ ions (Leidi *et al.*, 1991) and $NO_3^-$ ions present in soil solution (Arghavani *et al.*, 2017). Some plant species (pea, sunflower and maize) shown tolerance with $NO_3^-$ nutrition in saline environment (Frechilla *et al.*, 2001; Rios-Gonzalez *et al.*, 2002) while $NH_4^+$ ions significantly improved salinity tolerance in sorghum and barley (Kant *et al.*, 2007; de Souza Miranda *et al.*, 2016). In addition, salinity tolerance was increased with equal concentration of $NH_4^+$ and $NO_3^-$ ions in tomato, periwinkle (*Catharanthus roseus*), faba bean, and sorghum (Zhonghua *et al.*, 2011; Kamel, 2012; de Souza-Miranda *et al.*, 2014).

### *$NH_4^+$-N and salinity interactions*

Plant tolerance to salinity stress is associated with the form of nitrogen availability in soil. The underlying mechanism could be as follows:

Plants perform nitrate ($NO_3^-$) assimilation in shoots whereas $NH_4^+$ assimilation takes in in roots in growth media. Therefore, the imbalance ions under salinity stress could disturb the $NH_4^+$ assimilation in $NH_4^+$ fed plants while these plants continue $NO_3^-$ assimilation under salinity stress. The nitrate application triggers the plants to open a malate-nitrate shuttle between roots and shoot responsible to get rid of ionic effect of

NaCl. The absence of this shuttle in $NH_4^+$ plants caused ion translocation problems under salinity stress (Lewis *et al*., 1989). The increased $NH_4^+$ ions present in soil greatly reduce the carbon uptake which further lowers the root development under salinity stress (Dluzniewska *et al*., 2007). Moreover, the provision of energy also reduces for $NH_4^+$ assimilation and $Na^+$ exclusion in salt stress.

In addition, the $NH_4^+$ toxicity caused leaf chlorosis, reduced photosynthesis, nutrient imbalance, alters plant metabolism and consequently it reduces crop yield. Plants produced high ROS through $NH_4^+$ nutrition than $NO_3^-$ fed plants (Lewis *et al*., 1989; Frechilla *et al*., 2001; Rios-Gonzalez *et al*., 2002). In addition, the $NH_4^+$ provision to sunflower increased the $Cl^-$ ion accumulation that significantly lowers the $K^+$, $Ca^+$ and $Mg^+$ uptake and reduced the salinity tolerance (Ashraf and Sultana, 2000). Contrary, $NH_4^+$ supplementation produced mild stress that triggers the stress-induced morphogenetic responses (SIMRs) which further increased salinity tolerance in in oranges (*Citrus sinensis* L.) (Fernández-Crespo *et al*., 2012). Initially, SIMRs produces $H_2O_2$ that act as a modulator of stress signals to initiate the stress tolerance adaptation in plant. Moreover, $NH_4^+$ supply maintain the increased $K^+$:$Na^+$ ions that restricts the uptake and translocation of $Na^+$ ions while higher concentration of $NH_4^+$ ions increased the $Na^+$ exclusion from plants under salinity stress (de Souza Miranda *et al.* 2013). The stimulation of $K^+$ depletion capacity by $NH_4^+$ might be associated with plasma membrane $H^+$-ATPase-mediated higher $H^+$ transport activity which improves plant tolerance to salinity (Alvarez-Pizarro *et al.* 2011). Furthermore, the $NH_4^+$ increased the antioxidant defense mechanism and osmotic adjustment by producing different osmolytes that increase the salinity tolerance in plants. $NH_4^+$ supplementation increased synthesis of various enzyme (guaiacol peroxidase, glutathione reductase, catalases and ascorbate peroxidase) to detoxify the $H_2O_2$ produced under salinity stress (Hessini *et al*., 2013). Lastly, less energy requires for uptake and assimilation of $NH_4^+$ ions that also produce antioxidant enzymes and other osmolytes which regulate the $K^+/Na^+$ homeostasis to enhance salinity tolerance in plants.

### *$NO_3^-$- N and salinity interactions*

In aerobic conditions, plants uptake $NO^{3-}$ that reduced into $NH_4^+$ ion prior to produce organic nitrogen compounds. This process involve energy that comes from ATP as; 20 mole ATP molecule uses per mole of $NO_3^-$ assimilation, $NH_4^+$ require only 5 mole ATPs (Salsac *et al*., 1987). Though, plant uptake $NO_3^-$ form of nitrogen as a scavenging mechanism from ion toxicity with $NH_4^+$ ion accumulation in plant body (Meng *et al*., 2016). $NO_3^-$ ions accumulates in vacuole that prevent plant from ion imbalance, improves plant nutrition and responsible for osmotic adjustment thus salinity tolerance improves with $NO_3^-$ accumulation than the uptake of more $NH_4^+$ ions (Irshad *et al*., 2002). Plant assimilates more $NO_3^-$ ion in shoot than $NH_4^+$ assimilation that takes place in root directly contacting with rhizosphere in saline soils. In addition, $NO_3^-$ ion translocate rapidly in shoot indicating the efficient translocation of assimilates in from root to shoot under salt stress (Crawford, 1995). Though, some studies reported that the $Cl^-$ ion reduced $NO_3^-$ intake from saline environment and impairs the salinity tolerance by antagonistic effect of anions (Kant *et al*., 2007), promote $Na^+$ uptake that accumulate in plant cell (Zhonghua *et al*., 2011) and reduced the WUE and carbon assimilation under salinity (Ashraf, 1999) (Figure 3).

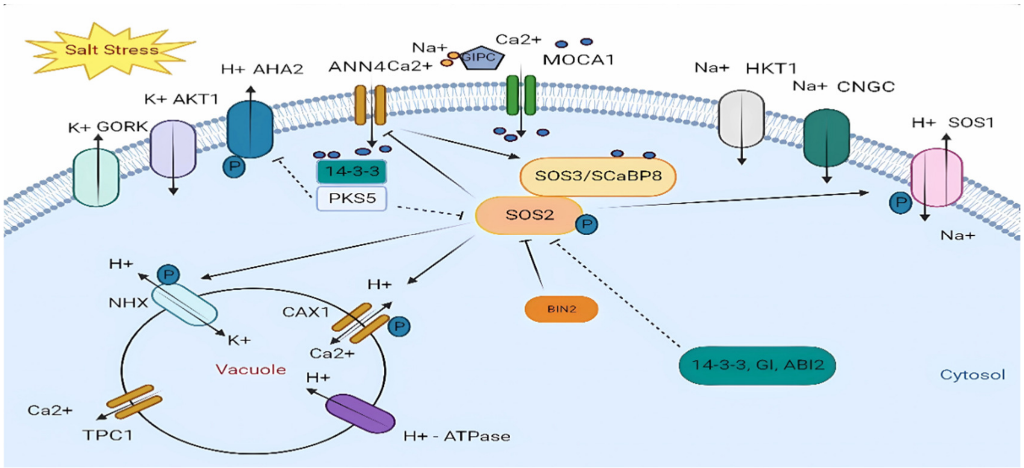

**Figure 3.** Salinity increases the $Na^+$ and $Ca^{2+}$ uptake in cell. MOCA1 allows $Ca^{2+}$ in plasma membrane. GIPC sphingolipids detect $Na^+$ and stimulate MOCA1-mediated $Ca^{2+}$ influx. $Na^+$ transport into the cell requires the CNGC and HKT1 channels. AKT1 and GORK maintain the $Na^+/K^+$ equilibrium. $Na^+$ exclusion requires the SOS pathway. SOS3/SCaBP8, the calcium sensor, binds SOS2 to the plasma membrane and phosphorylates the $Na^+/H^+$ antiporter SOS1. SOS2 inhibited by 14-3-3, ABI2, and GI normally inhibit. PKS5 also phosphorylates and inhibits SOS2. Salt stress degrades 14-3-3 and GI, releasing SOS2 to phosphorylate SOS1. While, 14-3-3 represses PKS5, activating SOS2. GSK3 and BIN2 fine-tune SOS2 activity to prevent overactivation during salt stress. ANN4, a potential $Ca^{2+}$ permeable transporter, controls calcium signaling under salt stress with SCaBP8 and SOS2. SOS2 stimulates the vacuolar $H^+/Ca^{2+}$ antiporter CAX1 to increase $Ca^{2+}$ and regulates NHX to maintain $K^+$ balance during salt stress. Arrows and bars represent positive and negative regulation. Solid and dotted lines show direct and indirect regulation, respectively. MOCA1: glucuronosyltransferase monocation-induced $Ca^{2+}$ increases 1, GIPC: glycosyl inositol phosphorylceramide, AKT1: arabidopsis $K^+$ transporter, GORK: guard cell outward-rectifier $K^+$ channel, SOS: salt excessively sensitive, ABI2: ABA insensitive, GI: Gigantea, PKS5: protein kinase 5, GSK3: gglycogen synthase kinase 3 and BIN2: brassinosteroid insensitive 2.

### *N-mediated mitigation of specific ion toxicity*

The adequate supply of essential nutrients mitigates the negative impact of ionic toxicity under salinity stress (Bahmanzadegan and Aboutalebi, 2013). Salt tolerance is associated with decreased absorption of $Na^+$ and $Cl^-$ ions in a saline soil, which could be possible through high absorption of $NH_4^+$ and $K^+$ ions (Table 1). High nitrogen in saline soil interacts with salt ions and decreased ion toxicity (Hütsch *et al.* 2016) and soybean (Guo *et al.*, 2017). The increased nitrogen supply augmented the $NO_3^-$ ions in saline soils that significantly reduced the $Cl^-$ intake by plant roots (Aroiee *et al.*, 2005; Iqbal *et al.*, 2015; Hütsch *et al.*, 2016). Moreover, the presence of high $NO_3^-$ ions dilutes the $Cl^-$ ions along with the antagonistic effect of two negative ions have been observed to stimulate the growth and decreased leaf abscission under salinity (Shawer, 2014). Many researchers reported the negative correlation of $NO_3^-$ and $Cl^-$ and positive effect of high $NO_3^-$ concentration on nitrogen uptake in different field crops under saline environment (Abdelgadir *et al.*, 2005; Tabatabaei and Fakhrzad, 2008; Bybordi *et al.*, 2010; Jabeen and Ahmad, 2011).

$NH_4^+$ compete with $Na^+$ ion at exchange site of soil, thus more uptake of $NH_4^+$ ion reduce the $Na^+$ toxicity (Fernández-Crespo *et al.*, 2012), improved $K^+$ uptake, and reduced the osmotic stress under salinity (Kant *et al.*, 2007). The $Na^+/H^+$ antiporters are responsible to maintain $Na^+$ concentration in root zone and also determines the effectiveness of nitrogen ($NH_4^+$) uptake from saline soil (Mansour, 2014). Therefore, various experiments suggested the optimum nitrogen supplement improved salinity stress tolerance by increased uptake of $NH_4^+$ ions and reduced $Na^+$ and $Cl^-$ ion toxicity in plants (Dubey *et al.*, 2021; Chen *et al.*, 2022).

*N-mediated maintenance of nutrient balance*

The ample supply of macro- (N, P, and K) and essential micro-nutrients (Zn, Fe, B and Mn etc) is key to enhance crop productivity. These nutrients involve in different physio-biochemical and morphological responses under abiotic stress (Rostami *et al*., 2018). Amongst these essential nutrients, nitrogen is imperative and its uptake, translocations, and distribution significantly reduced under saline conditions (Renault *et al*., 2016). The adequate nitrogen supply regulates ion homeostasis and improved salt tolerance (Khan *et al*., 2016; Zaki, 2016) (Table 3). Nitrogen application augments proline, GB and synthesis of soluble sugars, which in turn ensure the essential nutrients (P, K, Zn, Fe, B and Mn etc) uptake under saline conditions (Perveen *et al*., 2016; Hossain *et al*., 2020). The adequate nitrogen supply in saline soil regulates plasma membrane activity and maintain membrane stability indices confer the reduced negative effect of salinity and continues intake of nutrient from saline stressed soil (Khan *et al*., 2013; Singh *et al*., 2014; Parihar *et al*., 2015; Hossain *et al*., 2020; Kumar *et al*., 2021; Kumari *et al*., 2022).

High $Na^+$ and $Cl^-$ induced stress significantly reduced the $NH_4^+$, $NO_3^-$, $K^+$, $Ca^{2+}$ and $Mg^{2+}$ uptake by plant roots. Likewise, nitrogen supply in saline soil improved salinity tolerance and higher crop yield (Figure 4) (Dong, 2012; Khan *et al*., 2017). Contrary, many researchers found the nitrogen fertilization interacts and reduced NaCl intake, subsequently enhanced the $NH_4^+$, $NO_3^-$, $K^+$, $Ca^{2+}$ and $Mg^{2+}$ accumulation and thus improved salinity tolerance in plants (Table 3). In addition, the antagonistic effect of N ($NO_3^-$) with $Cl^-$ and $NH_4^+$ with $Na^+$ uptake observed under salt stress (Cámara-Zapata *et al*., 2004; Esmaili *et al*., 2008). Thus, the adequate nitrogen fertilization is significant to essential nutrient uptake, nutrient balancing, translocation that leads to salinity tolerance in plants.

**Table 3.** Mitigation of specific ion toxicity, oxidative stress and osmotic adjustment in crops mediated by nitrogen fertilization under salinity stress

| Crops | Salt stress | Nitrogen application | Effects | References |
|---|---|---|---|---|
| Cotton | 200 mm $L^{-1}$ NaCl | 2.5 mmol $L^{-1}$ | Nitrogen application increased the production of soluble proteins, sugars and free amino acid under salinity stress | Sikder *et al*., 2020 |
| Soybean | 100 mmol $L^{-1}$ NaCl | 15 mmol $L^{-1}$ | High nitrogen decreased the $Cl^-$ percentage in plants and led to significantly reduce in $Cl^-/NO_3^-$ ratio. Further, the nitrogen fertilization augmented more $K^+$ uptake from salt affected soil that positive correlate with osmotic balance that reduce the oxidative stress and ion toxicity in plants | Guo *et al*., 2017 |
| Mustard | 100 mM NaCl | 20 mM $NO_3^-$ | Nitrogen induced antagonistic effect significantly reduced the $Na^+$ uptake from salt affected soil. | Iqbal *et al*., 2015 |
| Cotton | 10 dS $m^{-1}$ | 100 mg N $kg^{-1}$ | Nitrogen supplementation significantly improved the $K^+$ uptake and $K^+/Na^+$ ratio, while reducing $Na^+$ intake from salt stressed soil | Khan *et al*., 2016 |
| Wheat | 100 mM NaCl | 100 mg N $kg^{-1}$ | Antioxidant defence system up-regulated by nitrogen fertilization that enhanced the osmolyte and secondary metabolite production to reduce the $H_2O_2$, SOD, POD, and lipid peroxidation in wheat under salt stress | Ahanger *et al*., 2019 |
| Pistachio | 2400 mg NaCl $Kg^{-1}$ soil | 180 mg N $kg^{-1}$ soil | The application of nitrogen significantly enhances the proline, reducing sugar, $Ca^{2+}$, | Nasab *et al*., 2014 |

| | | | | |
|---|---|---|---|---|
| | | | $Mg^{2+}$ help plants for ion homeostasis and osmotic adjustment under salinity stress | |
| *Populus cathayana* | 50 mM NaCl | 3.75 mM $NO_3^-$ | Ion homeostasis by higher uptake of $K^+$ ion resulted in more $K^+/Na^+$ ratio, followed by osmotic adjustment through higher root $Na^+$ efflux and lower root-to-shoot translocation of $Na^+$ was recorded with nitrate supply during salt stress | Liu *et al.*, 2022 |
| Rice | 140 mM NaCl (for 07 days) | 2 mM $KNO_3$ (for 07 days) | Application of nitrate (nitrogen) upregulated the specific gene (OsMADS27) responsible for ion homeostasis and antioxidation during salt tolerance | Alfatih *et al.*, 2023 |
| Grapes | 200 mmol $L^{-1}$ NaCl | 0.1 mol $L^{-1}$ $NH_4NO_3$ | Nitrogen fertilizer improved salinity tolerance through hormonal regulation during salinity by increasing the proline accumulation, total chlorophyll, and ion homeostasis with efficiency uptake of $NH_4^+$, and $NO_3^-$ concentration in plants | Zhang *et al.*, 2023 |

$Cl^-$, Chloride, $NO_3^-$, Nitrate, $K^+$, potassium; $Na^+$, sodium; $H_2O_2$, Hydrogen peroxide; SOD, Superoxide dismutase; POD, Peroxidase; $Ca^{2+}$, calcium ion; $Mg^{2+}$, magnesium ion; $NH_4^+$, amoniuum ion

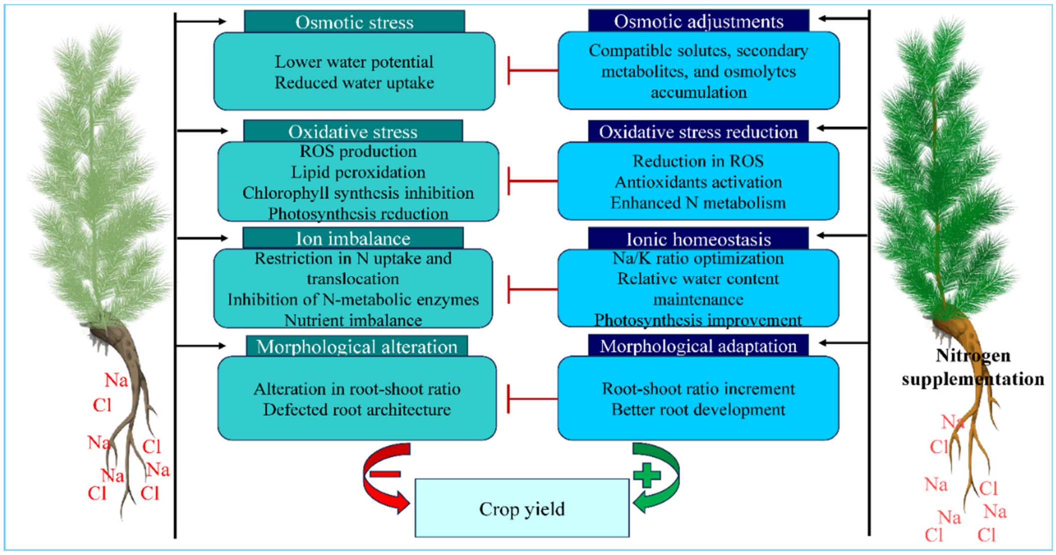

**Figure 4**. Nitrogen supplementation protects plant physiological and morphological machinery from salt stress, osmotic and oxidative damage. Nitrogen helps plants maintain ionic homeostasis and nitrogen metabolism amid salt stress, enhancing plant performance.

### *Nitrogen mitigates oxidative damage*

Plant produce different osmolytes in response the oxidative damage in salinity stress (Polesskaya *et al.*, 2006). Nitrogen is an integral part in structure of different osmolytes (glucose, sucrose, proline, GB, asparagine, sucrose, and glucose and dimethyl sulphoniopropionate). These osmolytes stabilize the photosynthetic pigmentation, prevent photosystem from damage and protein denaturing, decreased ROS production and improved membrane stability index (MSI) in salinity stress (Cuin and Shabala, 2007). Nitrogen contributes significantly in osmolyte production under salinity stress (Rais *et al.*, 2013; Fayez and Bazaid, 2014). Further, osmolytes augments more $K^+$ accumulation and increased $Na^+$ exclusion from plant cell helps to counteract the salinity stress (Sofy *et al.*, 2020; Seleiman *et al.*, 2020). These osmolytes includes glycine betaine (GB); proline

(Pro), soluble sugar, and amino acids. These are low molecular weight and water-soluble compound also known as compatible solutes neutralize the salt toxicity and oxidative damage in plants (Seleiman *et al.*, 2021). GB ($C_5H_{11}NO_2$) protect the photosynthetic machinery of plants from oxidative damage from oxidative damage by accumulation of high $Na^+$ salt during salinity. Moreover, GB involve in the maintenance of thylakoid membrane, protein and chlorophyll production of plants under salinity stress (Vineeth *et al.*, 2023) thus, regulate ROS scavenging program to mitigate the SS (Ashraf *et al.*, 2018). Likewise, proline ($C_5H_9NO_2$), a secondary amino acid and an important osmolyte under abiotic stress. Proline promotes the plant signaling after maintaining redox potential to improve salinity tolerance in plants (Nazir *et al.*, 2023). Proline based signaling is an adoptive mechanism that improve cytosolic pH, osmotic adjustment (Kavi Kishor and Sreenivasulu, 2014) and modifies the root system (Biancucci *et al.*, 2015) therefore, helps plant to grow best under salinity stress (El Moukhtari *et al.*, 2020; Osman and Naggar, 2022).

### *Nitrogen improves plant growth in saline environment*

The adequate supply of nitrogen to crop in saline conditions is vital to sustain the growth, development and productivity. Continues supply of nitrogen to crop growing under salinity bestow strength to plants against osmotic stress (Heidari *et al.*, 2011), stomatal opening (Akram and Ashraf, 2009), produce antioxidants (Fayez and Bazaid, 2014), alleviate ionic toxicity (Bahmanzadegan and Aboutalebi 2013), enhances nutrient uptake (Shawer, 2014), increase photosynthesis (Iglesias *et al.*, 2004), activates enzymes (nitrate reductase and carbonic anhydrase) (Rais *et al.*, 2013), stable the membrane permeability (Aragão *et al.*, 2012), and thus increases NUE (Bybordi *et al.*, 2010).

Moreover, continues nitrogen supply dilutes the salts in plant body that decrease the salt toxicity whereas the reduced leaf abscission due to ample N availability promote the plant growth consequently plant biomass increases. However, the root system has key role in exploiting the nitrogen status in soil as larger roots in adoptive mechanism absorbs more water and nitrogen from deeper soil layer to increase tolerance against soil salinity stress (Nhung *et al.*, 2017). In addition, the selectivity of plant nutrient absorption by plant roots and $Na^+$ ion exclusion from leaves increased with nitrogen nutrition (Kabir *et al.*, 2005), which increased the plant tolerance (Tabatabaei, 2006). Furthermore, the optimum nitrogen supply increased the $NO_3^-$ assimilation pathway that triggers the $CO_2$ fixation in *Jatropha curcas* (Aragão *et al.*, 2012), increased leaf proline contents in sugar cane (Nadian *et al.*, 2012), enhanced florescence and photosynthetic activity in maize (Akram *et al.*, 2010) and osmotic adjustments under salinity stress (Mansour, 2000). All these suggest that the optimum and continues supply of nitrogen decreased the leaf abscission, $Na^+$ and $Cl^-$ uptake, increased plant tolerance, growth and biomass under salinity stress.

## Conclusions

Salinity stress seriously reduced the plant growth and development by disturbing the physiological, biochemical and molecular functioning. Nonetheless, application of N improves plant performance under saline conditions by improving nutrient and water uptake, photosynthetic efficacy, antioxidant activities, and reducing oxidative damages and ionic toxicity. Therefore, the use of N fertilizers can be a useful tool to combat the salinity stress effects in plants. Though, there are still some research gaps in our understanding about the the role of N in inducing salinity tolerance in plants. The role of N in germination mechanisms are poorly studied, therefore it is important to determine how N affect the various mechanism of germination in plants growing under saline conditions. The role of N is nutrient uptake under saline conditions is also poorly studied in the literature, thus, more research is needed on this aspect.

The role of N in stomata movement is also not studied yet, thus, it is mandatory to study how N affect the stomata movements in plants growing under saline conditions. The role of N in signaling mechanism and functioning at tissue and organ level are not fully explained it is direly needed to understand the role of N in signaling crosstalk under salinity conditions. There is also missing information about the crosstalk of N with different hormones and osmolytes under saline conditions. Therefore, it is would be useful to unfold the crosstalk of N with hormones and osmolytes to induce salt tolerance in plants. It would also be fascination to reveal the effect of N on genes and enzymes involved in synthesis of hormones and osmolytes. Moreover, identification and analysis of key genes be effective to induce N mediated salinity tolerance which can provide a new framework to develop the crop varieties with improved salt tolerance and nitrogen use efficiency. Furthermore, the advent of genetic engineering technology holds significant promise for crop improvement and stress management.

## Authors' Contributions

Conceptualization, MTA, IK. MUC and MUH. Writing—original draft preparation, MTA, IK. MUC and MUH. Writing—review and editing, RM, MZH, WL, SU, AR, MUH, MH, ROE, MMQI and MA. All authors read and approved the final manuscript.

## **Ethical approval** (for researches involving animals or humans)

Not applicable.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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