

Innovations

Nitric Oxide: A Potential Molecule for Salt Stress Tolerance in Legumes

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Abstract: Salt stress is a significant environmental issue that affects growth and development of plants especially legumes, by reducing water potential, nutrient uptake, ionic imbalance, nodule potential etc. Higher concentrations of Na⁺ (sodium) and Cl⁻ (chloride) reduce the uptake of Ca²⁺ (calcium), K⁺ (potassium), and Mg²⁺ (magnesium) levels, and thereby, impacting the K⁺/Na⁺ ratio. Legumes activate their inherent salt tolerance mechanisms to maintain ambient environmental conditions for survival under salinity. These defense mechanisms involve biochemical and developmental changes, including ion homeostasis, accumulation of osmolytes, upregulation of antioxidant defense mechanisms, etc. However, in extended stressful situations, the oxidative burst of reactive oxygen species (ROS) outweighs the balance between ROS generation and scavenging, resulting in plant death as a result of cellular equilibrium being upset. Recently, various molecules have been exploited to impart tolerance to stressed plants, including gasotransmitters and signaling molecules like nitric oxide (NO), salicylic acid (SA), gallic acid (GA), hydrogen sulfide (H₂S), auxins, gibberellins, cytokinins, and abscisic acid. Among these, Nitric oxide (NO) is a crucial redox signaling molecule which improve growth and development of plants by boosting photosynthetic activity, respiratory rate, stomatal movement, ion homeostasis, osmolyte accumulation, leaf relative water content, etc. Keeping all this in mind, this review highlights the impact of NO in alleviating the detrimental effect of salt stress on leguminous plants and advocating for its application as a sustainable agricultural practice as it is efficient and ecofriendly to improve legume resilience against salinity and improve crop yield in saline environments.

Keywords: antioxidant enzymes, growth, legumes, nitric oxide, nutrient uptake, osmolytes, salt stress

Introduction

Legumes are nutritious crops which are rich source of proteins, vitamins, complex carbohydrates, and fibers. Leguminous plants have the ability to fix atmospheric nitrogen through forming the symbiotic relationship with bacterium; Rhizobium

(Zahran, 1999). Legumes are typically consumed by 21 people each day on a global scale (Semba et al., 2021). Grain legume production has been rising, with worldwide cultivation of pulses, groundnuts, and soybeans doubling from 148 million tons in 1980–1982 to 310 million tons in 2004–2006 (Gowda et al., 2009). However, in the past few decades, the increase in the incidence of abiotic stresses, resulted in significant reduction in the growth and productivity of legume crops. Therefore, there is a dire need to innovate some exogenous stress alleviators to the plants which can impart tolerance towards unfavorable environmental conditions, in a sustainable way. Abiotic stressors are the major environmental constraints which are posing a severe threat to the agriculturally important crops. Among the various stressors, salinity is one of the major abiotic factors that diminished the growth and productivity of plants (Tlahig et al., 2021; Bisht and Garg, 2022). Around 20% of irrigated land worldwide suffers from salt in their soil, which drastically lowers crop production (Qadir et al., 2014). Primary salinization refers to the organic buildup of salt in water as well as soil, resulting from processes such as weathering, wind, and precipitation. It is attributed to natural dynamics including hydrology, natural drought, aeolian salt deposition, and local parent rock materials. When irrigation or other agricultural methods cause the salinity of the surface soil to rise from non-saline to saline, this is known as secondary soil salinization (Peck and Hatton, 2003). However, due to the rise of salts brought on by an increase in ground water levels, desertification has resulted from secondary salinization brought on by the introduction of irrigation in arid regions. Due to soil salinity, crop yields have decreased by up to 50%, and as a result, many places have stopped farming (Swarajyalakshmi et al., 2003). Excessive accumulation of salt leads to various toxicity symptoms in the plant. The most prevalent cause of salt stress is elevated concentration of Na^+ and Cl^- ions. Higher amount of these ions lowers the water potential, create ion imbalances and leads to disruption of ionic homeostasis. In many plants, higher concentrations of Na^+ and Cl^- reduce the uptake of Ca^{2+} , K^+ , and Mg^{2+} levels which, thereby resulted in imbalance of K^+/Na^+ ratio (Parida and Das, 2005). Moreover, the reduction in biomass, leaf area, yield, stem size, and length of roots are also the major symptoms of salinity stress (Zorb et al., 2019).

Moreover, stressed plant exhibits higher production of reactive oxygen species (ROS), reduced activity of cytoplasmic enzymes, damaged cell structures, etc. (Valko et al., 2005). Overall, salinity stress induces various toxic responses in plants which, ultimately affect the normal growth and metabolism.

Plants have adopted various strategies to protect themselves from the damage caused by different environmental constraints. To overcome the negative impact of salt stress, plants use their complex natural salt tolerance mechanisms to maintain normal conditions that are needed for their survival. These processes include osmotic stress tolerance through the synthesis of osmolytes/organic solutes, ion homeostasis (Na^+ and Cl^- exclusion and/or compartmentalization, maintenance of tissue K^+/Na^+ ratio), and a variety of other biochemical and physiological

alterations (Khan et al., 2015; Singh et al., 2015). Additionally, plants use antioxidant defense mechanisms (enzymatic and non-enzymatic components) to eliminate the harmful effects of ROS produced by salt stress (Gill and Tuteja, 2010; Badran et al., 2015). Enzymatic antioxidants are a crucial defense mechanism against oxidative stress, employing enzymes such as SOD (Superoxide dismutase), CAT(catalase), POX (peroxidase), GPX (Glutathione peroxidase), etc.that dismutate O_2^- radicals into O_2 and H_2O . Ascorbate and glutathione are two non-enzymatic components that have been shown to be connected by the ascorbate-glutathione (ASA-GSH) cycle. They can immediately react with 1O_2 , O_2 , and OH^- , which greatly facilitates the scavenging of ROS without the use of enzymes (Hossain et al., 2013). However, under severe stressed condition, the oxidative burst of ROS synthesis will not be able to cease the ROS production and scavenging completely and thereby, disrupting cellular homeostasis (Abdel Latef and Miransari, 2014). Therefore, exogenous stress relievers are required to lessen the detrimental effects of salt stress on plants in a sustainable manner.

To negate the impact of abiotic stressors especially salinity, various molecules have been exploited to impart tolerance to the stressed plants. Among the various signaling molecules, Nitric oxide (NO) is a bio-active molecule and has an important function in plant growth and development. NO is a colorless signaling molecule and one of the principal oxides of nitrogen. Plant germination, development, flowering, senescence, and abiotic stress are some of the physiological processes in which NO, plays a crucial role (Nabi et al., 2019). NO also plays a role in nodule development and senescence in leguminous plants (Signorelli et al., 2020). Also, it has been observed that NO promote root growth, induce cell elongation, and mediate auxin response on plants (Stöhr and Stremlau, 2006). It is a key molecule during abiotic stress, which can modulate protein function and gene expression in plants (Fancy et al., 2017).

To the best of our knowledge, till date no review is available on the interactive impact of nitric oxide on legume crops under salinity stress. Keeping all this in mind, the current review tried to unravel the mechanisms by in imparting salt stress tolerance to the legumes by modulating various responses at physiological, biochemical and molecular level.

Effect of Salinity Stress on Legumes

In irrigated areas, salt stress has a detrimental effect on soil fertility and growth of legumes, endangering crop sustainability and productivity. Under salt stress plants display multiple changes at physiological, biochemical, and molecular level which is discussed in detail below:

1. Seed germination, growth and productivity

Seed germination is a vital process in plant development which, is inhibited by a number of stresses, including salinity. Various studies have been conducted to describe the detrimental effect of salinity on leguminous plants. In a study

conducted by Tsegay and Gebreslassie (2014), a negative impact of salt stress was reported on germination percentage, shoot length, and root length of *Lathyrus sativus* and *Pisum sativum*. Another study conducted by Lavrenko et al. (2019) found that increasing salinity levels reduced the growth and germination of chickpea seedlings. Lentil cultivar ILL6788 was reported to be more sensitive to salinity than Nugget during germination stage, highlighting the significance of taking salinity response into account at various growth stages (Rahimi et al., 2009). Similarly, a differential genetic response was recorded by Wu et al. (2011) in *Medicago sativa* and *Astragalus adsurgens* with *M. sativa* displaying more sensitivity to salinity during germination when compared to *A. adsurgens*. Ouji et al. (2015) reported detrimental impact of salinity stress on seed germination, growth, physiology and biochemistry of five different genotypes of lentil. On the same line, pea plants showed reduced seed germination, growth and biomass when treated with different level of salt stress (Petrović et al., 2016).

In addition to germination, salt stress also hampers the yielding potential of legumes by altering various physiological and biochemical processes. For example, faba bean exposed to different levels of salinity displayed reduced growth, grain number, number of pods and seed weight per plant (Tavakkoli et al., 2010; Katerji et al., 2011). Similarly, in pigeon pea plants salinity displayed a detrimental effect on reproductive growth in terms of reduced flower number, pod number, seed number, and seed weight (Ahmed and Ahmad, 2016). Another study conducted by Kaur et al. (2022) on chickpea revealed that the genotype PBG-7 was more affected by salinity stress than GPF-2 in terms of nodulation potential, nitrogen fixation, photosynthetic pigments, and growth, all of which ultimately affected the yielding potential of plant. Interestingly, salinity reduced biomass, number of branches, pods, seeds, relative water content, chlorophyll content and yield of lentil (Yasir et al., 2021). Overall, the studies confirm the negative impact of salinity on diverse growth parameter of legumes.

2. Photosynthesis, water and nutrient uptake

Photosynthesis is one of the physiological mechanisms influencing plant growth and crop productivity. Nutrients such as N, P, K, Mg, Ca etc., have direct role on the efficiency of photosynthetic process. A study conducted by Khan et al. (2010) correlated the reduced uptake of N, P, K, and Ca with decreased photosynthetic efficiency, water status and productivity of mung bean plants grown under NaCl toxicity. Another study by Latrach et al. (2014) revealed that salt stress had negative impact on growth, leaf water status, photosynthetic efficiency and yielding potential of *Medicago sativa* L. Similarly, *Medicago truncatula* displayed significant reduction in chlorophyll content, photosynthetic and transpiration rate, and stomatal conductance when treated with salt stress (Irshad et al., 2021). Tepary bean, cowpea, and wild bean plants displayed reduced height, leaf number, area and nutrient acquisition when treated with salinity stress (López-Aguilar et al., 2003). Faba bean plants showed reduction in transpiration efficiency, stomatal

conductance, rate of photosynthesis and nutrient uptake when grown under salt stressed environment (Tavakkoli et al., 2010; Benidire et al., 2017; Benmoussa et al., 2022). Salinity stress altersthe K^+/Na^+ ratio in the leaves of faba bean which ultimately responsible for lowering of photosynthetic efficiency of plants (Ma et al., 2024). Pea plants exhibited higher stomatal density, stomatal diffusive resistance, and decreased water and nutrient content in roots, stems, leaves, pods, and grains, when exposed to salinity stress (Maksimović et al., 2010). Another study by Rahman et al. (2022) explored the role of Na^+/H^+ exchangers and Na^+/K^+ transporter genes in sodium homeostasis and lignin biosynthesis and observed that high Na^+ accumulation disrupted the metabolic processes, growth and productivity of alfalfa plants under salt stress. These investigations showed how salt stress impairs photosynthesis as well as absorption of nutrients and water of legumes.

3. Nodulation potential

Nodulation potential refers to a plant's capacity to produce root nodules, which are necessary for nitrogen fixation with the help of symbiotic relationship between legumes and nitrogen-fixing bacteria (rhizobia). Salt stress significantly impacts rhizobial symbiosis and results in reduced rhizobial growth, infection, nodule formation, and nitrogen fixation (Zahran, 1999). For example, exposure of soybeans to salt stress displayed a significant reduction in nodule number, dry weight and quality of nodules (Singleton and Bohlool, 1984). Similarly, salt stress negatively affected legume-rhizobial symbiosis in faba bean plants and thereby, a significant decline was reported in nodule number and biomass (Benmoussa et al., 2022). Moreover, in *Phaseolus vulgaris* a dramatic reduction in acid phosphatases (APase) activity was reported by Faghire et al. (2013) in nodules under salinity stress indicating the harmful impact of the salt stress on rhizobial symbiosis. Chickpea plants had a substantial negative impact on the nodulation potential and nitrogen fixation efficiency when treated with salt stress (Sadji-Ait Kaci et al., 2017). On the same line, *M. officinalis* displayed negative impact on growth and rhizobial symbiosis when grown under salt affected environment (Bruning et al., 2015). In addition to nodulation potential, trehalose metabolism has also been reported to be affected by salinity in leguminous plants. Pigeon pea plants exposed to salinity displayed higher activity of trehalose-6-P synthetase (TPS) and trehalose-6-P phosphatase (TPP) enzymes which resulted in increased amount of trehalose in nodules (Garg and Chandel, 2011). Another study on *Lotus japonicus* showed that salinity affected trehalose content in plants, with nodules displaying 40% increase in trehalose content (Lopez et al., 2006). In *Medicago truncatula* and *Phaseolus vulgaris* salinity reduced the activity of trehalase enzyme which resulted in higher accumulation of trehalose in nodules (Lopez et al., 2008). In a study conducted by Garg and Pandey (2016) on *Cajanus cajan* plant under salinity stress revealed increased accumulation of trehalose in nodules due to decreased trehalase activity and increased TPS and TPP activities. Overall, the research supports the idea that

salinity has a detrimental effect on legumes' ability to develop nodules as well as trehalose metabolism.

4. Oxidative and osmotic stress

In leguminous plants, oxidative stress occurs due to an imbalance between generation of ROS and the plant's capacity to detoxify them, leading to cellular damage and potentially death, especially under stressed conditions. Various reports are available on the induction of oxidative stress under salt stressed environment especially in legumes. For example, salinity stress exacerbated the oxidative stress in chick pea plants by increasing the production of ROS, MDA (malondialdehyde) content and led to protein degradation (Keshvkant et al., 2012). Amirjani (2010) assessed the effect of salinity stress on soybean plants and reported higher ROS accumulation and reduced antioxidant enzymes activity. Another study by Alharbi et al. (2022) discovered that elevated salt levels in pea plant resulted in higher ROS production and cell damage ultimately affected the cell membrane integrity. In soybeans, prolonged exposure to salinity stress resulted in elevated levels of cellular hydrogen peroxide (H_2O_2) which ultimately responsible for cell death (Egbichi et al., 2014). Similarly, in *Lotus japonicus* the lipid peroxidation (MDA) level was increased which related in the oxidative damage of the plants due to salt stress (Rubio et al., 2009). Khator et al. (2020) concluded that *Cyamopsis tetragonoloba* and *Vigna radiata* when subjected to salt stressed displayed increased MDA and H_2O_2 levels which thereby resulted into increased oxidative stress. Similarly, in chick pea plants the levels of MDA and H_2O_2 increased due to salinity stress (Dadaşoğlu, 2022).

Along with oxidative stress, osmotic stress occurs due to salinity also affect the legumes by reducing water uptake and thereby, leading to cell dehydration, changes in turgor pressure, and ultimately impacting plant growth and yield. A study conducted by Tavakkoli et al. (2010) on faba bean plants concluded that there is a decrease in the leaf osmotic potential when treated with NaCl. When the legumes common bean, broad bean, and alfalfa were grown under salt stressed conditions, a significant improvement was recorded in proline content which is an indicator of osmotic stress (Razi and Khadhir, 2021). Similarly, higher accumulation of proline was recorded in soybean plants when treated with varying concentration of salinity (Amirjani, 2010). When common bean plants were exposed to salinity, the contents of total soluble sugars, free proline and glycine betaine (GB) increased significantly (Rady et al., 2013). Another study conducted by Panuccio et al. (2022) on lentil plants revealed a significant increase in proline content which, in turn helped the plant to maintain redox balance under saline conditions. In contradictory, Atta et al. (2022) reported a significant reduction in proline content when rice bean plants treated with salt stress. According to these findings, salinity has a harmful impact on oxidative and osmotic stresses of legumes.

Table1: Effect of salinity stress on various species of legumes

S.No	Host Plant	Concentration of Salt	Impact of Salt Stress on Legumes	Reference
1.	Vigna spp.	0, 50 mM and 100 mM	Reduced germination percentage, germination rate, shoot length, root length and seedling dry weight	Awasthi et al. (2016)
2.	Phaseolus sp.	0, 60 and 90 mM	Reduced growth, photosynthesis and leaf osmotic potential	Bayuelo-Jiménez et al. (2012)
3.	Phaseolus vulgaris	50, 100, 150, 200, 250 and 300 mM	Reduced seed germination and seedlings growth	Mena et al. (2015).
4.	Vigna radiata	50 mM and 75 mM	Reduced root and shoot growth, chlorophyll and carotenoid contents	Sehrawat et al. (2015)
5.	Phaseolus vulgaris	0.3, 0.6, 0.9, 1.2, and 1.5 MPa	Decreased germination rate, germination percentage and seed vigour index	Cokkizgin (2012)
6.	Arachis hypogaea	0.5 and 3.5 dS m ⁻¹	Reduced growth and biomass	Sá et al. (2019)
7.	Vigna mungo and Vigna radiata	50, 75 and 100 mM	Reduced grain yield	Karim et al. (2001)
8.	Arachis hypogaea	0 mM, 50 mM, 100 mM, 150 mM, 200 mM, and 250 mM	Decreased shoot height, number of plants, root length, fresh and dry weight	Satu and Ahmed (2019)
9.	Vigna angularis	100 mM	Reduced growth, biomass accumulation, photosynthesis, chlorophyll synthesis, gas exchange parameters, and photochemical efficiency	Ahanger et al. (2019)

			(Fv/Fm)	
10.	<i>Pisum sativum</i>	0, 50 and 100 mM	Decreased chlorophyll a and b content, fresh-dry weight, relative water content (RWC) and K ⁺ /Na ⁺ and Ca ²⁺ /Na ⁺ ratio	Dadasoglu et al. (2021)
11.	<i>Vicia faba</i> L.	0, 60, and 120 mM	Reduced shoot biomass, nodulation potential and nitrogen content	Benidire et al. (2017)
12.	<i>Phaseolus vulgaris</i> L.	control, 5, 10, 20 and 40 mmol ⁻¹	Decreased plant root and shoot dry weight, chlorophyll content, plant height, root length, total nitrogen content and inhibited the symbiotic efficiency	Uyanöz and Karaca (2011)
13.	<i>Vicia faba</i> L.	0.0, 60, 120, 240 mM	Reduced plant height, osmotic potential, chlorophyll a, b and carotenoids content	Qados (2011)
14.	<i>Vicia faba</i> L.	50 mM, 100 mM, and 150 mM	Reduced growth, biomass yield, and antioxidant content	Alzahrani et al. (2019)
15.	<i>Lathyrus sativus</i> L.	0, 50, 100 and 200 mM	Reduced seedling length, and increased phenolic compounds, membrane integrity, antioxidant enzyme activity, and proline content	Piwowarczyk et al. (2016)
16.	<i>Glycine max</i>	80 mM	Decreased biomass of shoots, roots and nodules, increased cellular hydrogen peroxide content and cell death	Egbichi et al. (2014)

17.	<i>Phaseolus vulgaris</i>	75 and 150 mM	Decreased growth, photosynthesis, osmolyte contents (proline and glycine betaine) and increased oxidative damage	Dawood et al. (2022)
18.	<i>Glycine max</i>	50 mM	Reduced germination and early growth of seedlings	Kataria et al. (2020)
19.	<i>Cicer arietinum</i>	0, 40, 60, and 80 mM	Decreased plant growth and AM symbiosis	Garg and Bharti (2018)
20.	<i>Vicia faba</i> L.	0, 90, 120, 150 and 200 mM	Decreased germination percentage, fresh and dry weight of seeds	Anaya et al. (2018)

Role of NO under Salt Stress in Legumes

Nitric oxide (NO) is a key factor of increasing growth and development of plants by boosting the growth, photosynthetic activity, respiratory rate, stomatal movement, ion homeostasis, etc. (Shang et al., 2022). Moreover, it improves osmolyte accumulation, leaf relative water content, and antioxidative defense system and thereby, lessen the impacts of salt stress on plants (Ahmad et al., 2016). Some of the roles of NO under salinity stress has been discussed in detail below:

1. Growth, nutrient and water uptake

Seed germination and growth of legumes has negatively impacted by salinity which, in turn can be mitigated with the application of NO. Multiple NO donor is now being explored by researchers to improve the growth and productivity of plants under diverse abiotic stressors. For example, a study conducted by Ahanger et al. (2019) found that the application of NO significantly reduced the intensity of oxidative damage in salt stressed *Vigna angularis* by enhancing the growth, photosynthetic parameter and boosting the antioxidant defense machinery. According to Salahuddin et al. (2017), mung bean germination and seedling growth were greatly enhanced by exogenous application of sodium nitroprusside (SNP; which is a NO donor). Similarly, the positive impact of SNP was reported by Yasir et al. (2021) in alleviating the detrimental impact of salt stress on growth and yield-related parameter of lentil. On the same line, increased seed germination percentage and decreased mean germination time were recorded in SNP treated common bean plants (Elkoca et al., 2016). Another NO donor i.e. S-nitroso-N-acetyl-D,L-penicillamine (SNAP) enhanced the germination percentage and growth

of chickpea seedlings exposed to salinity (Pandey et al., 2019). Interestingly, 2,2'-(hydroxynitrosohydrazono) bis-ethanimine (DETA/NO) which, is another NO donor improved the germination, growth and various biochemical attributes in salt stressed soybean plants (Egbichi et al., 2014). Overall, above mentioned studies indicate that NO acts as a potential growth regulator in negating the impact of salt stress on germination and growth parameters of legumes.

Along with growth and germination, NO also have the ability to increase the nutritional and water status of plants which thereby can also dilute the impact of salt stress on legumes. For example, when salt stressed soybean plant was treated with SNP, a significant increase in K^+/Na^+ ratio was observed due to consumption of K^+ and reduction of Na^+ content (Karthik et al., 2019; Jabeen et al., 2021). Similarly, a significant reduction in K^+/Na^+ and Ca^{2+}/Na^+ ratios observed in salinity treated pea plants which was nullified by the exogenous application of NO (Dadasoglu et al., 2021). Exogenous application of NO in lupin plants resulted in a considerable increase in uptake of divalent cations (Ca^{2+} and Mg^{2+}) and K^+ ions, and reduced the uptake Na^+ ion (Hashem et al., 2023). Application of NO to chickpea plants enhanced the water uptake, RLWC, growth and yield when grown in salinity stressed soil. (Dadaşoğlu, 2022). In salt stressed *Vigna angularis* plant the exogenous application of NO individually or cumulatively with SA reduced the accumulation of Na and Cl content and increased N, K, and Ca content (Ahanger et al., 2019).

2. Photosynthesis and productivity

Photosynthesis is a vital process for plant growth and can be affected by salt stress while NO plays a key regulatory role in mitigating the harmful effects of this abiotic stressor. For example, exogenous application of NO improved chlorophyll content and growth of pea cultivars when grown under salt contaminated soil (Dadasoglu et al., 2021). Similarly salt stressed chickpea plants displayed higher chlorophyll level, photosynthetic efficiency as well as the productivity when treated with NO (Ahmad et al., 2016; Dadaşoğlu, 2022). According to the study conducted by Yasir et al. (2021), a significant improvement was recorded in chlorophyll pigment, photosynthesis and yielding potential of salt stressed lentil plants supplemented with NO. Foliar application of SNP lessened the negative effect of salt stress on cowpea plants by improving the levels of chlorophyll a, b, total chlorophyll, and carotenoids and thereby enhanced the photosynthetic efficiency of plants (Eisa and Ibrahim, 2016). Similarly, the detrimental impact of salinity stress on growth and photosynthesis of lupin plants were eliminated by the exogenous application of NO (Hashem et al., 2023). Moreover, exogenous application of SNP raised the chlorophyll a and b contents by 38% and 44% respectively, in salinity stressed soybean plants (Jabeen et al., 2021). On the same line, salt stressed *Vigna angularis* plants showed increased photosynthetic and transpiration rates when treated with exogenous NO individually as well as cumulatively with SA (Ahanger et al.,

2019). These studies depicted that the exogenous application of NO can mitigate the salt stress by enhancing the photosynthetic parameters and yield of the plants.

3. Osmolyte accumulation

NO encourages osmolytes accumulation like proline and soluble sugars under salt stress, which can help the plants to deal with osmotic stress. In a study conducted by Ahmed et al. (2016), NO imparted osmotic homeostasis to salt stressed chickpea plants by improving the accumulation of proline, GB, total soluble proteins and total soluble sugars. Similarly, lupin plants displayed higher synthesis of osmolytes such as soluble sugars, polysaccharides, and organic acids, specifically malic, succinic, formic, acetic, and butyric acids when supplemented with SNP under salt stress (Hashem et al., 2023). Exogenous application of SNP led to the higher proline, sugar and GB contents in *Pisum sativum* grown under saline stress (Yadu et al., 2017). Similarly, seed priming of *Vigna radiata* with SNP displayed a significant improvement in the level of proline, reducing sugars and total amino acid under salinity stress (Roychoudhury, 2021). Application of SNP led to higher RWC and proline levels in salinity stressed soybean plants (Karthik et al., 2019). Interestingly, individual as well as cumulative application of NO and SA displayed higher accumulation of osmolytes (proline, sugars, and glycinebetain) in salt stressed *Vigna angularis* (Ahanger et al., 2019). All these studies indicate that NO can alleviate the detrimental impact of salt stress on legumes by upregulating the synthesis of various osmolytes.

4. Antioxidant defense

NO plays an important role in plant antioxidant defense under salt stress by controlling ROS levels, and modulating the activity of antioxidant enzymes. Ahmed et al. (2016) revealed that NO shielded the chickpea plants from oxidative damage brought on by salt stress by boosting the production of antioxidant enzymes, strengthening growth metrics, and lowering the electrolyte leakage. Similarly, salinity stressed *Pisum sativum* plants displayed reduced buildup of ROS, MDA, 4-hydroxy-2-nonenal, and protein carbonyl and higher activity of SOD, CAT, GPX and APX enzymes when supplied with SNP (Yadu et al., 2017). Moreover, NO improved POD, SOD, and APX activities in salinity-stressed pea cultivars (Dadasoglu et al., 2021). In soybeans, when NO treatments, either as DETA/NO alone or in conjunction with NaCl is applied then APX enzymatic activity increased significantly, which imparted redox homeostasis to the plants (Egbichi et al., 2014). Seed priming with SNP alleviated salt-induced oxidative and ionic stress in *Vigna radiata* by improving the activity of antioxidative enzymes and thereby, enhanced the seedling tolerance and survival capacity (Roychoudhury, 2021). In soybean plants SOD, CAT, POD, APX, PPO (Polyphenol oxidase) and PAL (Phenylalanine ammonia-lyase) activity increased in root and leaf tissues under salinity stress which was further improved by exogenous application of SNP (Jabeen et al., 2021). Ahanger et al. (2019) reported that in *Vigna angularis*, the foliar application of NO

individually or cumulatively with SA significantly decreased H_2O_2 , O_2^- , MDA, EL, and LOX activity. Similarly, exogenous application of SNP significantly reduced the oxidative stress in salt stressed lupin plants (Hashem et al., 2023), depicting that NO acts as a potential stress ameliorator in negating the impact of oxidative stress on legume plants.

Cross Talk of NO with Other Signaling Molecules

NO is a potential molecule for mitigating the harmful effects of salinity stress in plants individually strengthening the antioxidant defense, improving osmotic regulation, and modulating ion transport (Shang et al., 2022). However, when combined with other molecules such as SA, γ -aminobutyric acid (GABA), caffeic acid and sodium hydrosulfide (NaHS), NO has been reported to improve plant growth, stress tolerance, and overall physiological performance under saline conditions. Researchers are now exploring the combined effect of NO with other molecules which show better ameliorating effect towards salinity stress. For example, a study by Ahanger et al. (2019) investigated that NO and SA shielded the *Vigna angularis* from oxidative damage by increasing growth, photosynthetic parameters and antioxidant system activity when grown under salinity stressed area. Similarly, another study by Yadu et al. (2017) on salt stressed *Pisum sativum* reported that the combined effect of SA and SNP improved the growth, development, and metabolism and thereby, imparted tolerance to stressed plants. Moreover, in soybean plants when treated with GABA promoted the phenolic compound synthesis, with NO and thereby neutralized the effects of salt stress (Xie et al., 2021). Exogenous application of NO and caffeic acid in salt stressed soybean plants led to reduced accumulation of excessive ROS by upregulating the antioxidant defense machinery (Klein, 2012). Interestingly, NaHS boosted the production of endogenous NO and alleviated the effect of salt stress on *Medicago sativa* plants by increasing the activity of antioxidant enzymes (Wang et al., 2012). Another study by Simaei et al. (2012) revealed that the exogenous application of SA and SNP shielded soybeans from salt stress by increasing nutrient uptake and antioxidative enzymes activity.

Conclusion

Salinity stress negatively affects seed germination, growth, productivity, photosynthesis, nutrient and water uptake, and nodulation potential in leguminous plants. However, NO emerges as a key player in mitigating the detrimental effects of salt stress on legumes. Exogenous application of NO improves growth and productivity of legumes by enhancing nutrient and water uptake, photosynthesis, osmolyte accumulation, and strengthening antioxidant defense. Furthermore, the individual as well as cumulative application of NO with other signaling molecules such as polyamines, hormones etc. shows promising roles enhancing growth and stress tolerance of legumes under saline conditions. However, the molecular mechanism behind the potential roles of NO in mitigating the impact of salt stress in

lacking which needs further attention. Moreover, further studies are required to unravel the mechanism of action of NO under realistic field condition. Overall, application of NO to legume plants proved to be efficient; eco-friendly and sustainable agricultural practice.

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