



Salinity Stress in Legume Crops: A Comprehensive Review of Effects, Mechanisms, and Mitigation Strategies

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Article Information

DOI: <https://doi.org/10.9734/jsrr/2024/v30i72189>

Open Peer Review History:

This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: <https://www.sdiarticle5.com/review-history/119415>

Review Article

Received: 01/05/2024

Accepted: 04/07/2024

Published: 05/07/2024

ABSTRACT

Salinity stress poses a significant challenge to global crop production, particularly in regions relying heavily on irrigation. This review explores the detrimental impacts of salt stress on grain legumes, crucial plants renowned for their high protein content and nitrogen-fixing ability. The increasing use of saline groundwater and the accumulation of soil salts threaten the sustainability of legume cultivation worldwide. Salt stress disrupts fundamental physiological processes in legumes, including photosynthesis, hormone regulation, and nutrient uptake, resulting in substantial reductions in yield and quality. It exacerbates osmotic stress and ion toxicity, severely compromising plant health and productivity. Understanding the intricate mechanisms underlying salt

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Cite as: Chaudhary, Sahil B, Deshraj Gujjar, Bijendra Kumar, Smit Patel, and Simran. 2024. "Salinity Stress in Legume Crops: A Comprehensive Review of Effects, Mechanisms, and Mitigation Strategies". *Journal of Scientific Research and Reports* 30 (7):783-99. <https://doi.org/10.9734/jsrr/2024/v30i72189>.

tolerance in grain legumes is pivotal for developing effective mitigation strategies. This review synthesizes current knowledge on the tolerance mechanisms employed by legumes to cope with salt stress. It examines various management approaches aimed at enhancing their resilience under saline conditions. Key findings highlight that salt stress can lead to over 70% reductions in growth and variable decreases in yield and mineral absorption rates. Innovative strategies such as genetic engineering of transgenic varieties and advanced crop management practices offer promising avenues to enhance salt tolerance and boost legume productivity on salinity-affected soils. Furthermore, insights into mechanisms such as ion compartmentalization and ion excretion provide critical pathways for developing salt-resistant legume cultivars. Apoplastic acidification emerges as a reliable indicator of salt stress resistance in these plants. By elucidating these mechanisms and strategies, this review contributes to the ongoing efforts aimed at safeguarding legume production and global food security in the face of escalating salinity stress.

Keywords: Salinity stress; physiological; resilience; apoplastic; resistance; food security.

1. INTRODUCTION

Salt-affected soil may have excess soluble salt and commutable sodium at the soil's level or in the rhizosphere. Salinity stress, which impacts more than 800 million hectares of land worldwide, is one of the primary obstacles to the development of profitable crops. Inaccurate agricultural trails have contributed to an increase in salt attentiveness in the rhizosphere, together with environmental variables such as parent rock pollution, sea salt, and salty beach water [1]. The productivity of arable land under cultivation is at risk due to the global increase in salinization of arable land. According to Deinlein [2], oxidative damage and nutritional imbalances fall under the same category as salt stress for glycophytes as do osmotic stress and ionic imbalances. While Cl, the main anion in salt-affected soils, may also be hazardous to certain plant species, Na is the most potentially harmful ion under these conditions. Plant hydration is restricted by a "physiological/secondary drought" resulting from a "osmotic balance imbalance" caused by elevated salinity levels [3].

Fabaceae include low-cost, high-nutrient foods, such grain legumes. These consist of 17–40% of the proteins included in food, as well as significant amounts of fibre, complex carbohydrates, vitamins, minerals, and important amino acids. Legumes are an important part of crop rotation because they have the biological capacity to fix nitrogen (N), which increases crop yields and enhances soil fertility. Legumes are unique in that they provide various living things with a skeleton of nitrogen (N) due to their ability to fix nitrogen (N) from biologically limiting molecular dinitrogen (N₂) to accessible forms. Legumes comprise 12–15% of all arable land worldwide and provide 27% of major

agriculture and 33% of dietary protein [4]. Because they are abundant in protein, legumes constitute a staple diet for millions of people and animals.

The effects, mechanisms of tolerance, and management of salt stress in grain legumes have not been adequately addressed, despite the fact that the effects of salt stress on numerous crops have been researched [2,3,5,6]. This article reviews and synthesises the impacts of salt stress on grain legumes, including how it affects nutrient intake, hormone control, senescence, grain growth, leaf development, carbon fixation, and light harvesting. The processes behind the tolerance to salt are explained. Moreover, a variety of management techniques, in conjunction with recently created breeding and functional genomics technologies, are being researched to increase grain legumes' resistance to salt stress.

1.1 Saline Soils

The excessive amount of saltwater soluble in these soils is hazardous to most plant development. According to the Soil Science Society of, the general categorization limit is $EC_e > 4 \text{ dS m}^{-1}$, while the minimum values for pH and SAR are less than 8.5 and 13 (mmolCl^{-1}) $1/2$, respectively. Although suspensions of greater soil to water ratios (1:1, 1:2, or 1:5) are also utilised, the electrical properties of the extract of saturated paste (EC_e) is typically used to determine the salinity of the soil. However, there are significant differences between various plant and crop kinds, as well as under varying soil and climatic situations, and the critical limit of $EC \ 4.0 \text{ dS m}^{-1}$ is merely arbitrary. These soils' structure and other physical characteristics remain unaffected.

1.2 Saline Sodic Soils

The majority of plant growth is threatened by these soils' significant saltwater soluble component. The overall classification limit is $EC_e > 4 \text{ dS m}^{-1}$, while the minimum values for pH and SAR are less than 8.5 and 13 (mmolcL^{-1})^{1/2}, respectively, according to the Soil Science Society of The electrical characteristics of the extract of saturated paste (EC_e) are often employed to calculate the salinity of the soil. But larger soil to water ratio (1:1, 1:2, or 1:5) suspensions are also helpful. However, the EC_e 4.0 dS m^{-1} critical limit is completely arbitrary, and there are large differences between different plant and crop species as well as under different soil and climatic circumstances. The physical properties and content of these soils don't change.

1.3 Salinity Effect on Transpiration, Photosynthesis, Plant Growth and Crop Yields

These soils have pH values larger than 8.5 and EC_e and SAR values greater than 4 dS m^{-1} and 13 (mmolcL^{-1})^{1/2}, respectively. Changes exist in the ratios of soluble salts (EC_e) and exchangeable sodium (assessed by SAR or ESP). These soils are relatively porous at first, but when soluble salts from raindrops or irrigation water seep through, sodium becomes more abundant and the physical characteristics of the soil progressively take on characteristics of a sodic soil. As a result, these soils have characteristics with both sodic and saline soils.

1.4 Legumes and Salinity/Sodicity

Salinity has an impact on plant development and productivity, depending on the kind of plant, salinity levels, and ionic composition of the salts. The majority of agricultural plants produce less when irrigated with salted water or in more salinized soils; this results in discernible alterations in plant growth patterns. Many different types of salinized ecosystems are home to plants. On the other hand, species that are more resistant to salt, like cotton, may only exhibit a 20% dry weight drop, while sensitive plant families, like soybean, may perish at the same concentration of NaCl.

2. EFFECT OF SALT STRESS ON GRAIN LEGUMES

Grain legumes are very susceptible to salt stress, which significantly lowers production, as Table 1

illustrates. Salinity is a critical risk factor for the formation of root nodules, plant germination and development, the symbiotic relationship with Rhizobium, and legumes' ability to fix nitrogen, according to Van [7]. Reduced carbon fixation [8], imbalanced hormone regulation, nutritional deficiencies, specific ion and osmotic effects [9,10], delayed flowering, and decreased flower numbers and pod set are some of the factors linked to salinity-induced yield reduction. Here, the impacts of salt stress on legume grain production and quality are discussed, along with their effects on seed germination, seedling establishment, nutrient absorption, carbon fixation, and light harvesting. Fig. 1. Illustrated the Influence of salt stress on the growth of different chickpea genotypes.

2.1 Germination and Plant Growth

By reducing water intake and/or negatively affecting the embryo, salt exposure prevents germination [3,11]. A reduction in the water potential gradient between the surrounding environment and the surface is the main barrier to dramatic growth [12]. Salt stress limits water absorption, the first step in germination, but also accelerates the enzymes that break down food reserves and initiate the germination metabolism. Furthermore, salt inhibits the mobilisation of starch, delaying the development of the embryonic axis. For example, in cowpea (*Vigna unguiculata* L.), salt stress significantly reduced seed germination by decreasing the activity of the hydrolytic enzymes α - and β -amylase [13]. Secondary seed dormancy may also be brought on by osmotic stress from salt. Higher intracellular concentrations of Na and Cl during the dividing and developing stage limit cell metabolism [14,15] states that grain legumes are significantly more susceptible to salt stress during the establishment of seedlings and later stages of development than they are during germination. This is consistent with the biphasic paradigm put out by Munns [16], according to which ion toxicity occurs in the second phase while osmotic stress inhibits development in the first. Since starch is mostly mobilised during the establishment phase, legume seeds are particularly vulnerable to salt stress. Chickpea (*Cicer arietinum* L.) development decreased significantly at extremely low salt concentrations (20 mM), but it decreased by 71% at 25 mM NaCl, as shown by Sadiki [17]. Other grain legumes were also reduced by salt stress: faba bean (*Vicia faba* L.; [18]; common bean (*Phaseolus vulgaris* L.; [19];

mungbean (*Vigna radiata* (L.) Wilczek; [20]; lentil (*Lens culinaris* L.; [21]; soybean (*Glycine max* L.; [22]; and lentil (*Lens culinaris* L.; [21]. Reduced tissue water potential, or less water accessible to cells, is often linked to

these growth declines [23,24]. Garg [25] claim that this inhibits growth, decreases photosynthesis, and induces stomatal closure. Fig. 2 shows bi-phasic model of salinity-induced growth reduction.

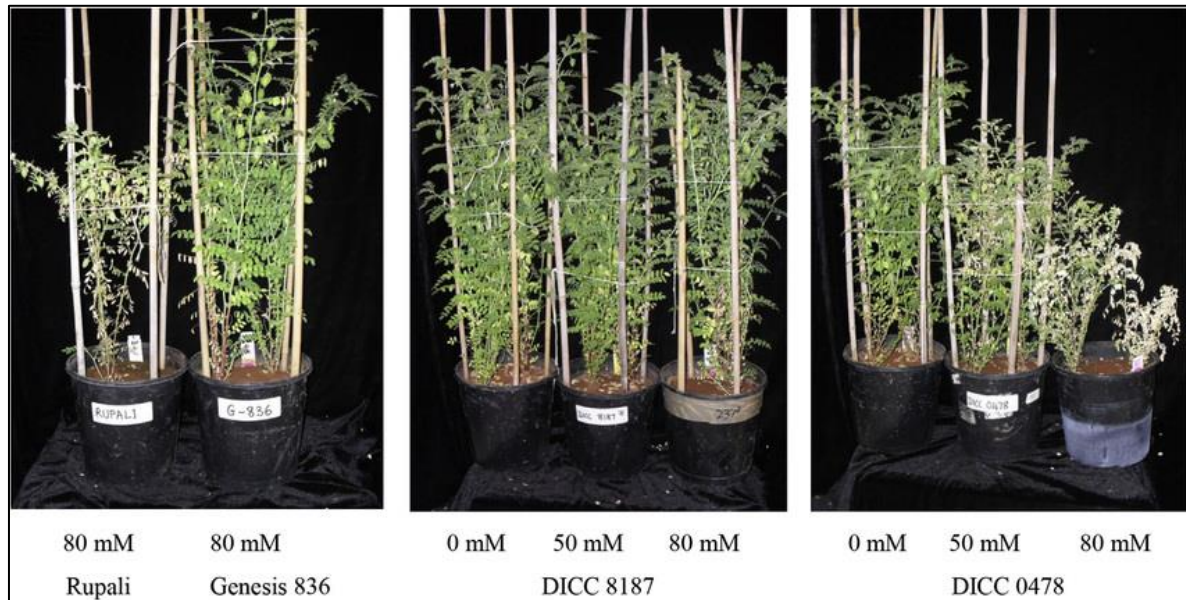


Fig. 1. Influence of salt stress on the growth of different chickpea genotypes. Genotype DICC 8187 performed better under salt stress than the other genotypes

Table 1. Yield reduction under different salinity levels

Legume Crops	Salt Concentration	Yield Loss (%)	References
Soybean (Galarsum)	14.4dSm-1	50%	[30]
Soybean (clay soil)	3.8dSm-1	29%	[7]
Soybean (loam soil)	7dSm-1	46%	[7]
Soybean (caly soil)	6.3dSm-1	46%	[31]
Mungbean (cv. Pusavishal)	50	41%	[32]
Mungbean (var. 245/7)	8dSm-1	60%	[33]
Mungbean (var. NM-51)	12dSm-1	77%	[33]
Mungbean (var. NM-92)	8dSm-1	61%	[33]
Mungbean (var. 6601)	12dSm-1	72%	[33]
Chickpea (var. FLIP 87-59)	3.8dSm-1	69%	[31]
Chickpea (var. FLIP 87-59)	2.5dSm-1	43%	[7]
Chickpea (var. ILC 3279)	3.8dSm-1	72%	[7]
Fababean (loam soil)	6.6dSm-1	50%	[31]
Fababean (clay soil)	5.6dSm-1	52%	[31]
Fababean (loam soil)	4.9dSm-1	28%	[7]
Fababean (clay soil)	4.3dSm-1	19%	[7]
Lentil (cv. 6796)	3.1dSm-1	100%	[7]
Lentil (cv. 6796)	2dSm-1	14%	[7]
Lentil (cv. 5582)	2dSm-1	24%	[7]
Lentil (cv. 5582)	3.1dSm-1	88%	[7]

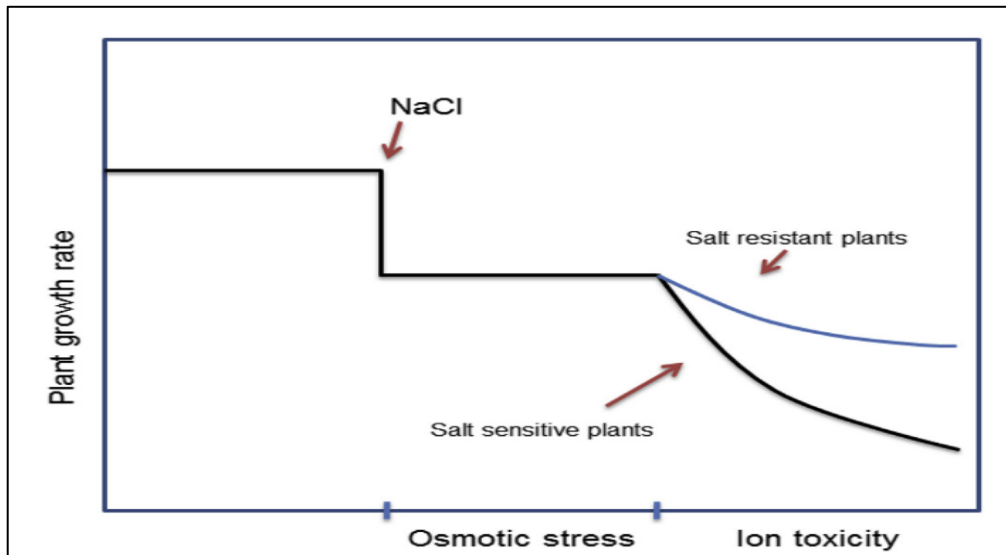


Fig. 2. A bi-phasic model of salinity-induced growth reduction [16]

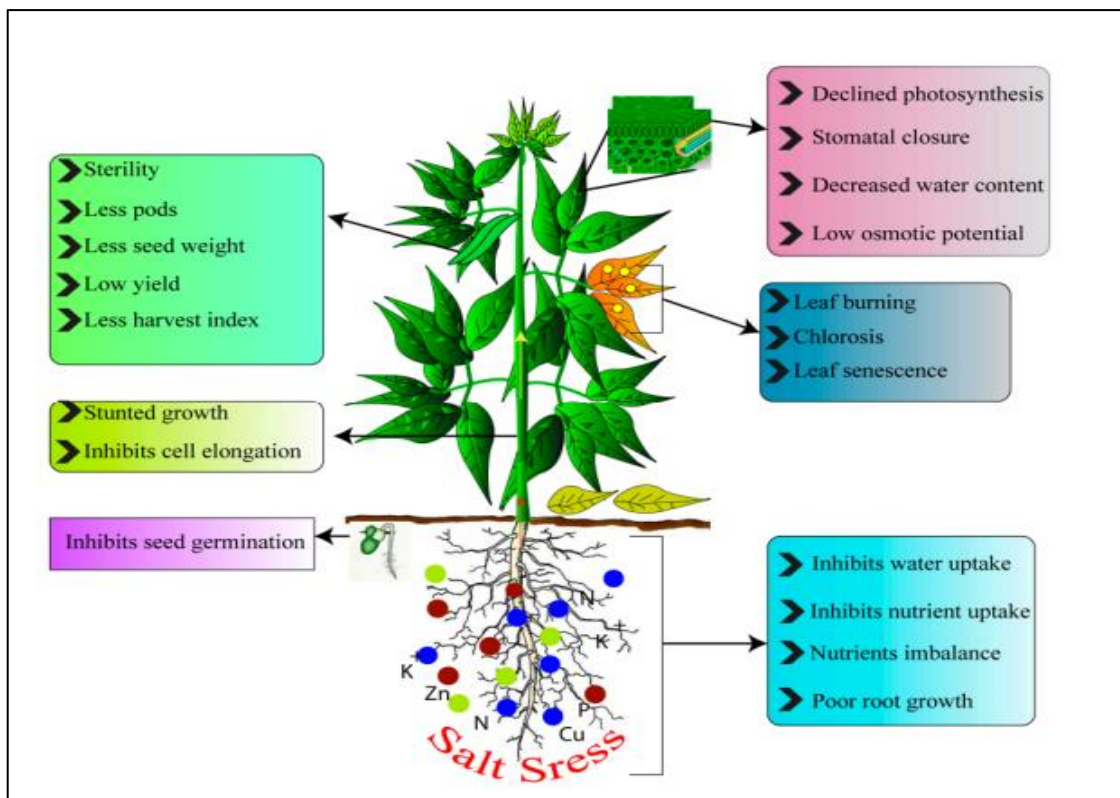


Fig. 3. Schematic representation of plant response to salt stress

Lower growth rates in grain legumes under salt stress have also been related to lack of cell wall acidification [18]. Apoplastic acidification, which is caused by plasmalemma H-ATPase activity and the activation of pH-dependent cellular-wall-loosening enzymes involved in cell growth and enlargement, facilitates growth stimulation [26].

Thus, as the faba bean demonstrates, inhibiting the acidity of the cell wall slows down the growth of new cells. Another mechanism attributed to salinity-induced growth decreases in grain legumes is specific ion toxicity [16,27]. One way to characterise this component would be as a function of tissue Na and/or Cl ion concentrations

and time. Ion poisoning is the main cause of salt stress-induced leaf death, according to Samineni [27]. When chickpea plants were cultivated in 20 mM NaCl, their growth was reduced by as much as 17%; in this instance, it was Cl, not Na, that passed the threshold concentration and caused the harm. Shoot had more Cl than Na at a greater concentration of NaCl (60 mM) [27]. Chouhan [28] found no correlation between shoot Na and chickpea development under salt stress, in contrast to Vadez [29]. In conclusion, when grain legume seeds are subjected to salt stress, a number of processes, including as ion toxicity, osmotic stress, decreased water absorption, turgor loss, lack of apoplastic acidification, and/or specific ion toxicity, inhibit the seeds' ability to germinate. It also prevents them from developing Fig. 3. Illustrated the schematic representation of plant response to salt stress.

Grain development and yield formation: Salt stress suppresses physiological responses and morphological features, which hinders grain legume growth and decreases yields by 12–100%, according to Flowers [5], Khan [30], and others (Table 1). The main factors that determine grain yield in grain legumes are the weight of each grain, the number of pods per plant, and the number of grains per pod. According to Dhingra [34], Mamo [35], salt stress lowers pollen production and flower counts, which in turn lowers pod counts, grains per pod, and grain weight. Both within and across species, there is variation in this area [34,36,5]. Reduced stigma receptivity, decreased pollen viability, and a lack of photo assimilates during grain filling are the three main factors causing salinity-induced decreases in grain production [5,30]. For example, chickpea under salt stress had significantly lower grain yields because the pollen tube shortened, resulting in less grains and less fertilisation [34]. [36] discovered that pollen viability was unrelated to salinity-induced increased pod abortion in sensitive chickpea genotypes, since salt stress had no effect on *in vitro* pollen germination or *in vivo* pollen development. According to several studies [36,37,38] there was no appreciable increase in the concentration of Na⁺ in reproductive tissue that would have had an adverse effect on the mechanisms involved in reproduction. Since grain growth is primarily supported by assimilates from the current photosynthesis in leaves (photosynthates produced after anthesis provide up to 98% of the grain carbon in grain legumes), this salinity-induced pod abortion may be related

to a significant reduction in assimilate supply under salt stress [30]. Even while the grain weight in chickpeas only drops by 20% or 10%, grains grown under salt stress may shrink and lose part of their grain protein, according to [29] and [39]. However, other yield components are declining as well: the quantity of grains falls by 33.50%, and the number of pods decreases by 38% [29,39]. Lower grain weights and fewer grains per pod were the primary causes of salinity-induced decreases in mungbean grain production [33,40,33]. However, in soybeans, the yield loss caused by salt was equally attributable to every yield-related trait [41]. "Salinity-induced osmotic stress causes oxidative stress, which disrupts the integrity of biological membranes and reduces the carboxylation rate. Increases in tissue Na and Cl cause ion toxicity, which decreases leaf growth, and triggers early leaf senescence, which reduces the carboxylation rate. Salt stress also reduces photosynthesis due to a reduction in the activities of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEP Case), and NADP-malic enzyme (NADP-ME). Non-cyclic electron transport is also down-regulated to match the reduced requirements of lower nicotinamide adenine dinucleotide phosphate production, which reduces the synthesis of adenosine tri-phosphate" (Fig. 4) [15].

2.2 Light Harvesting and Carbon Fixation

Research by Flexas [8], Khan [42], Chaves [43], and others has shown the significant impacts of salt stress on grain legumes. Both stomatal and non-stomatal components may be responsible for this decrease (Fig. 4; [42,43]). Legumes' capacity to fix carbon (C3 photosynthesis) is lowered in response to salt stress because of decreased stomata diffusion and resulting CO₂ availability (Flexas et al., 2004). Non-stomatal reasons include oxidative damage to the photometric apparatus and mesophyll conductance to CO₂. For instance, in chickpea, the cause of the fall in photosynthesis under salt stress was damage to photosystem II (PS II) rather than stomatal restriction, or a drop in the concentration of CO₂ between cells. Moreover, oxidative stress resulting from salinity and/or toxicity from Na and/or Cl could have played a part [42]. Hernandez [44] confirmed a same discovery in pea. Eyidogan [45] found a correlation between a decrease in photosynthesis in chickpea under salinity and non-stomatal factors, namely oxidative damage to the thylakoid.

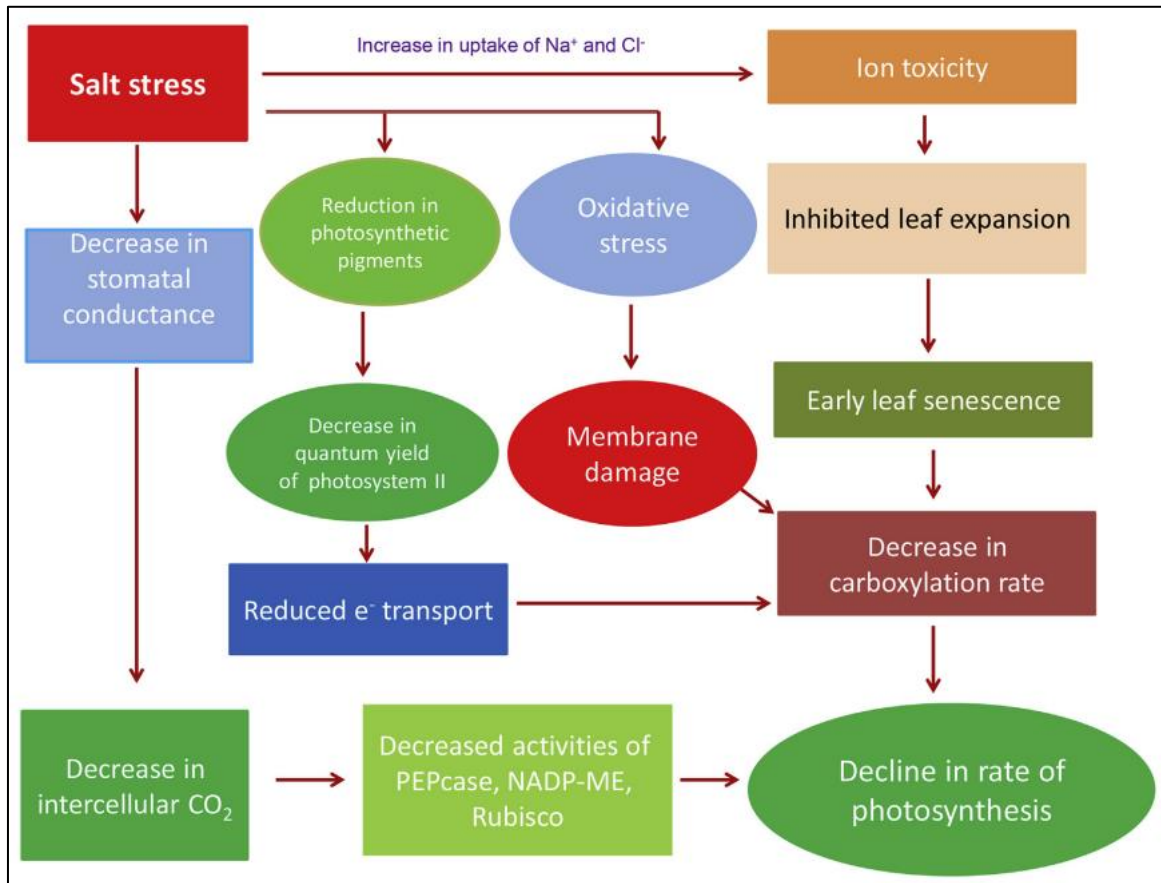


Fig. 4. Mechanism of salt stress-induced reduction in the rate of photosynthesis [15]

Salt stress causes an overabundance of reactive oxygen species, or ROS, which in turn causes oxidative stress. Reduced CO₂ intake causes photorespiration in legumes, which stimulates cell membrane-bound NADPH oxidases and apoplastic diamine oxidases, resulting in excessive H₂O₂ synthesis in the peroxisome. In the Calvin cycle, reduced stomatal conductance minimises CO₂ intake and minimises water loss. This leads to the release of oxidised NADP⁺, the last electron acceptor, and the start of electron leakage, which forms O₂ [46]. These mechanisms lead to the generation of ROS. One area of cell biochemistry that is impacted by elevated ROS production is membrane permeability. Plants' vital physiological processes are hampered by the oxidative damage that salinity-induced ROS production does to lipids, proteins, and DNA, among other cellular components [47]. Although there is currently a dearth of study on legumes, it has been shown that certain species respond to salt stress by releasing both reactive oxygen species (ROS) and nitrogen reactive elements (NRS). Many stomatal and non-stomatal factors, including as reduced photosynthetic pigments,

ultrastructural degradation, and chlorophyll fluorescence, contribute to salinity-induced decreases in photosynthesis in grain legumes [45,42].

2.3 Biological Nitrogen Fixation

By obstructing the biological fixation and absorption of N, salt stress lowers the amount of N accessible in grain legumes [48,49]. In plant roots, specialised structures known as nodules emerge where biological N fixing occurs. However, since nodules involved in biological N production are susceptible to salt stress, the nodulation process is very vulnerable to it. For instance, salt stress dramatically decreased the quantity and activity of nodules in faba bean [50,49] and pigeon pea (*Cajanus cajan* L.) [25] due to their premature senescence [51], which inhibited biological N fixation [50,52].

Rhizobia stimulate the formation of legume nodules in saline conditions, where they engage in molecular interactions with symbiotic partners. Moreover, proper rhizobia chemotaxis may get

flavones or isoflavones, which are plant metabolites. When rhizobia approach the roots, they increase the expression of many genes associated with lipochito-oligosaccharide synthesis and secretion; these genes are called NOD factors (NFs) [53,54]. Alfalfa (*Medicago sativa* L.), peanuts (*Arachis hypogaea* L.), peanut butter (*Arachis truncatula* Gaertn.), peas, soybean, faba bean, and common beans (*Phaseolus vulgaris* L.) are among the legumes that are more susceptible to salt than others [55]. Thus, host plants are more vulnerable to salt stress than *Rhizobium*, according to Manchanda [56], whereas Mudgal [57] discovered that functional symbiosis is particularly vulnerable to salt stress. When faced with salt stress, Zahran [58] said, "Better findings can be obtained for symbiotic N fixation if partners have mutual symbiosis and various other steps between their interaction (nodule formation/development, activity, etc.) oppose salt stress."

In grain legumes, salt stress often affects symbiotic relationships and plant growth [59,60]. The suppression of particular nitrogenase activity is one technique to illustrate the deleterious consequences of salt stress on the legume-*Rhizobium* symbiotic relationship. According to Delgado [61], bacteroids and protein haemoglobin were found to be decreasing, which resulted in a reduction in nitrogenase activity. Reduced availability of vitamin C, mostly as malate, worsens the harm that salt does to bacteroids. This may be due to the fact that salt inhibits some enzymes, including phosphoenolpyruvate carboxylase and sucrose synthase. This implies that the oxygen supply to the nodules is one of the limiting variables. As salinity rose, a tolerant *Rhizobium*'s increased oxygen nodule conductance stability was connected to higher salt tolerance [62].

2.4 Ion Homeostasis

Ion homeostasis, which is controlled by ion flux regulation to maintain low concentrations of detrimental ions like Na^+ and high concentrations of essential ions like K^+ , is a crucial property of live cells under salt stress [63,3]. Maintaining intracellular (K^+ and Na^+) homeostasis is necessary for regulating cell volume, protecting membrane potential, and enabling the proper function of many cytosolic metabolic enzymes [63]. Plants maintain a balance between intracellular K^+ and Na^+

concentrations in salinity by removing excess salt from the cytosol via primary active transport as well as secondary transport pathways. [63,64].

To maintain ion homeostasis in the face of salt stress, plant cells control these sodium transporters in the tonoplast and plasma membrane [64]. The transcript levels of many K^+ transporter genes vary with salinity [65]. Extruding or compartmentalising excess Na^+ in the vacuole is an effective strategy to counteract the detrimental effects of Na^+ in the cytoplasm [64,3]. Ion distribution patterns vary across grain legume species and cultivars, particularly with respect to the cytosolic Na^+/K^+ ratio [65]. For instance, the salt-tolerant mashbean cultivar (T-44) has special Na^+/K^+ transporters that help to maintain low intracellular Na^+ concentration [4]. Pigeon peas have a mechanism for salt tolerance that involves enhanced K^+ absorption, maintaining high K^+/Na^+ ratios in shoots, and keeping Na^+ and Cl^- out of shoots, according to Waheed [66]. Munns [12] suggest that ion toxicity in reproductive organs and younger leaves may be prevented by ion sequestration in older tissues and the exclusion of Na^+ and Cl^- by roots. According to Turner [36], there is a significant correlation between chickpea salt sensitivity and higher Na^+ concentrations in immature leaves and seeds, but not in later tissues. Salt tolerance requires limiting the build-up of excess Na^+ in younger tissues; however, this may not be connected to ion storage in older tissues [36]. Accumulation of osmolytes in different grain legumes under salt stress tabulated in Table 2.

Because Na^+ and K^+ are exchanged at the xylem/symplast boundary of the roots, Na^+ may move from the transpiration stream into the xylem parenchyma cells under salt stress [75]. This exchange depends on anion permeability, which is supported by high apo plastic Concentrations, the plasma membrane H^+ -ATPase, and the Na^+/H^+ and K^+/H^+ antiporters [76,77]. The vascular H^+ -ATPase and H^+ -Pases activity in tonoplast vesicles of a salt-tolerant soybean variety increased under salt stress compared to a less tolerant variety [78]. In summary, one of the most important ways that plants resist salt is by getting rid of extra Na^+ and Cl^- ions or separating them into vacuoles or older tissues. This might lessen the negative consequences of increased Na^+ content and osmotic potential, which could aid grain legumes in osmoregulation.

Table 2. Accumulation of osmolytes in different grain legumes under salt stress

Crops	Osmolytes	Traits	References
Chickpea	Proline Total soluble sugars, proline, glycine and choline	Energy-yielding substrates for Bacteroides Improved plant biomass and photosynthetic pigments	[67] [68]
Faba bean	Free amino acids and free proline	Osmotic adjustment	[10]
Groundnut	Proline	Osmotic adjustments and protection of membrane integrity	[69]
Kidney bean	Glycine betaine	Increased stomatal conductance and leaf RWC	[70]
Mungbean	Potassium accumulation in leaf, root, and stem	Increased survival tolerance, leaf RWC, membrane stability index, grain weight and grain yield	[71]
Pea	Reducing sugars, total free amino acids, and ascorbic acid Potassium and calcium	Osmotic adjustment Increased root and shoot dry weights	[72] [73]
Pigeon pea	Leaf proline	Tolerance to salinity	[74]

2.5 Hormone Control

Plant hormones, often known as phytohormones, are substances that regulate plant development. Important plant hormones include auxins, cytokines, gibberellins (growth promoters), ethylene, and ABA (growth retardants). During salt stress, alterations in ethylene and ABA—sometimes known as stress hormones—are often seen. For instance, the white lupin (*Lupinus albus* L.) closed its stomata in response to ABA produced locally; subsequently, after salt stress, it changed its response to ABA produced by the roots and transferred to the leaves [79]. Elevated levels of ABA affect stomatal oscillations in leaves and other tissues, but they also help plants adapt to salt by adjusting osmotic pressure and producing certain stress proteins associated with salt tolerance [80]. Kukreja [81] reported that ethylene and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) were created by salt-stressed chickpea and faba bean roots and nodules. These compounds promoted leaf senescence but were not associated with appreciably quicker growth. Consequently, changes in stress hormone levels brought on by salt stress have an impact on photosynthesis, osmotic adjustment, and plant growth.

3. MANAGEMENT STRATEGIES

To increase grain legume output in salted environments, production technology must be used to modify genotypes of various grain legumes that are salt-tolerant. The next section discusses methods for enhancing grain legume yields under salt stress and enhancing salinity tolerance.

3.1 Selection and Traditional Methods of Breeding

Salt tolerance is a complex trait from a genetic and physiological perspective. There aren't many accessible and useful methods for determining grain legumes' salt tolerance. The capacity of grain legumes to tolerate salt has not significantly improved using conventional breeding methods [82]. An integrated approach that utilises genetic variation already present [83], generates new variation through novel and diverse sources [84], and uses a historical breeding approach with multiple traits instead of breeding for a single trait [85] may be helpful when creating genotypes of salt-resistant legumes. Fortunately, different species of legumes have different salt tolerances [86]. This variety may be used by breeders to create genotypes of legumes resistant to salt. To

locate salt-tolerant germplasm for breeding, legume genotypes are often screened extensively, allowing for the production of better genotypes. In the first phases of seedling development, evaluated 11 mungbean genotypes' capacity to withstand salt. Despite significant variations in their decreased germination and early seedling development, the genotypes under inquiry were classed as highly tolerant, tolerant, moderately tolerant, sensitive, moderately susceptible, and very vulnerable [71]. To screen for salt tolerance, a variety of characteristics have been examined, including plant biomass, nodulation, osmotic adjustment, leaf K/Na/Ca ratios, pod number per plant, grain weight, and grain yield (Table 3). Stress tolerance has been increased by traditional breeding methods including Na⁺ exclusion [82]. Tissue ion homeostasis is a critical characteristic that is used to evaluate genotypes for resistance to salt stress [12]. But it hasn't been shown how tolerance and individual Cl⁻ or Na⁺ "exclusion" relates to other grain legumes like chickpea. Due to the accumulation of potentially hazardous levels of Na⁺ and Cl⁻ during the reproductive phase, chickpeas are particularly vulnerable to salt stress [27].

However, due to salt stress, no correlation was found between yield and the accumulation of Na⁺ (% dry mass) in shoots during the

vegetative stage [29]. A number of mechanisms, including tissue tolerance of excess ions and ion exclusion, seem to contribute to the at least moderate tolerance of chickpeas and other grain legumes to salt. However, breeding operations incorporating parental lines with varied origins are necessary to develop genetically modified genotypes that are salt-tolerant in other grain legumes, such as mungbean [87]. Grain output in salinized conditions is the ultimate test of salt tolerance; thus, characteristics that measure salt tolerance must be linked to grain yield [5]. Thus, a mass screening for salt tolerance might be carried out based on plant biomass, homeostasis, osmotic adjustment, and grain production in a salinized environment.

3.2 Biotechnology and Functional Genomics

The genes responsible for salt tolerance are widely distributed in the genomes of legumes (Table 4). Finding pertinent trait QTLs and marker tagging are necessary for targeted introgression, which combines salt-tolerant features into unadopted traits (Table 4). The readily available databased sequences have made whole genome sequences (WGS) the basis for newly developed simple sequence repeats (SSRs), single-nucleotide polymorphism

Table 3. Potential traits/characters for screening grain legumes for salinity resistance

Crops	Traits/Characters	References
Faba bean	Leaf soluble proline	[10]
Chickpea	Surge in nodule growth	[89]
	Total nitrogenase activity and nodule dry weight	[90]
Cowpea	Plant biomass	[91]
Kidney bean	Stomatal conductance	[70]
Mungbean	Survival	
	Photosynthetic pigments	[71]
	Pods per plant	
	100-grain weight	[32]
Pea	Rate of photosynthesis	
	Leaf reducing sugars	
	Total free amino acids	[72]
	Seedling emergence	
	Plant biomass	[73]
	Leaf K ⁺ /Na ⁺ ratio	
	Leaf Ca ²⁺ /Na ⁺ ratio	
Pigeon pea	Leaf soluble proline	[92]
Soyabean	Leaf soluble proline	
	Leaf K ⁺ contents	[93]
	Leaf Na ⁺ contents	
	Nodulation	[94]
	Osmotic adjustment	

Table 4. QTLs for salt tolerance identified from various grain legumes with their respective traits

Crops	Character	QTLs	Linkage Group	References
Chickpea	Days to flowering	TA114-TA78		[95]
	Shoot dry weight	TA127-TS57		
	Seed number	TR20s-TA46		
	100- seed weight	TR20s-TA46		
Pea	Salt tolerance index	Salt index_QTL 1	Ps III	[96]
	Symptoms of salt tolerance	Symptom	Ps III	
	Salt tolerance index	score_QTL 1		
		Salt index_QTL 2	Ps VII	
Soyabean	Percentage plant survival	qppsB2.1	B2	[97]
		qppsD1bpW.1	D1bpW	
		qppsK.1	K	
		qppsN.1	N	
	Plant survival days	qpsdB1.1	B1	
		qpsdK.1	K	
		qpsdG.1	G	
	Salt tolerance ratings	qtrG.1	G	
		qtrM.1	M	
		qtrM.2	M	

(SNP) markers, and next-generation sequencing techniques; as a result, the efficiency and cost-effectiveness of molecular marker-based crop improvement have increased recently. Soybean is one such grain legume where genotyping by sequencing has been made simpler to enhance salt tolerance. Additionally, studies have looked at the possibility of using genetic markers to identify important QTLs in order to produce cultivars with improved salt tolerance (Table 4). One research discovered that the sequence was differentiated by an amplified regions marker (QS08064), two SSR markers (Barcsoysr-3-1306 and Barcsoysr-3-1310), and an InDel marker (QS080465) when crossing two farmed soybeans, Tiffing 8 (tolerant) and 85-140 (sensitive). On chromosome 3, this area and the salt-tolerance gene co-segregated [88]. Moreover, a significant QTL on chromosome 17 was linked to Na⁺ tolerance; a robust association between salinity tolerance and the SSR markers indicated that SSR markers might be useful in marker-assisted selection. QTLs between the markers sat 255 and sat-091 on chromosome 3 were examined in soybean.

By creating 38 distinct microsatellite markers (SSRs), [71] produced twelve genotypes of mungbeans—nine cultivated and three wilds—that were diversified enough to withstand salt. Of the 124 possible alleles, 65 (52.42%) were detected in the cultivated genotypes, 52 in the wild genotypes (interspecific), and 100 in the heterogeneous (interspecific, 80-65%) category where the cultivated and wild genotypes were

combined. The polymorphism ranged from 86.84 to 100%, and the number of polymorphic alleles varied from 1 to 4, with an average value of 2.63 per locus. Significant QTLs or genes that confer salt tolerance may be found using these SSRs. Additionally, in order to tailor salt-tolerant mungbean hybrids for locations affected by salt, breeding initiatives may take use of the genotypes of naturally occurring salt-resistant plants as a source of beneficial traits or genes. Breeding strategies that prioritise early genotype selection over phenotypic screening may find value in the SSRs associated with the phenotype or genes [98].

Covarrubias [99] report that evidence of mi-RNA accumulation in common beans during drought or in response to ABA supplementation has been found. Their role in salt stress, however, has not been studied. However, in mature soybean root nodules generated under and without salinity stress, it was shown that mi-RNAs were up-regulated, suggesting that they actively control salt stress [100]. To synthesise the required quantitative or qualitative traits, one or more genes from one species are substituted for another using a transgenic technique. This approach is more effective than traditional breeding and guarantees that just the required genes from donor species are induced.

4. CONCLUSION

Salt stress is the biggest barrier to the development of good crops, especially in areas

where salty irrigation water is utilised. Legumes derived from grains are an excellent source of protein and have the potential to fulfil the needs of expanding populations in the future. On the other hand, the majority of grain legumes rely heavily on salt stress. Salinity causes osmotic stress, specific ion effects, poor hormone regulation, nutritional imbalances, and reduced carbon fixation in legumes due to stomatal and non-stomatal restrictions. These impacts all negatively affect grain production and quality. Strategies to improve grain legume performance in saline environments may be developed by recognising other management options and understanding the resistance mechanisms associated with the response of grain legumes to salt stress. Legume crops respond to salt stress by altering both their catalytic and non-enzymatic antioxidant defence systems, hormone control, osmoregulation and osmotic balance, and detrimental ion exclusion mechanisms, among other things. In salinity-prone areas of the world, it is necessary to develop salt-tolerant genotypes of different grain legumes using precise and location-specific production techniques in order to sustainably boost legume output. However, transgenic legume genotypes that are more adapted to salinity-affected areas may be introduced via the fusion of modern genomics and biotechnology research with conventional breeding techniques. This complex feature will be better understood and clarified with the identification of putative salinity-responsive genes in a variety of grain legumes, further research on upstream and downstream components, and a thorough examination of gene expression at various developmental stages using more advanced technologies.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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