



Salt stress responses and alleviation strategies in legumes: a review of the current knowledge

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Abstract

Salinity is one of the most significant environmental factors limiting legumes development and productivity. Salt stress disturbs all developmental stages of legumes and affects their hormonal regulation, photosynthesis and biological nitrogen fixation, causing nutritional imbalance, plant growth inhibition and yield losses. At the molecular level, salt stress exposure involves large number of factors that are implicated in stress perception, transduction, and regulation of salt responsive genes' expression through the intervention of transcription factors. Along with the complex gene network, epigenetic regulation mediated by non-coding RNAs, and DNA methylation events are also involved in legumes' response to salinity. Different alleviation strategies can increase salt tolerance in legume plants. The most promising ones are Plant Growth Promoting Rhizobia, Arbuscular Mycorrhizal Fungi, seed and plant's priming. Genetic manipulation offers an effective approach for improving salt tolerance. In this review, we present a detailed overview of the adverse effect of salt stress on legumes and their molecular responses. We also provide an overview of various ameliorative strategies that have been implemented to mitigate/overcome the harmful effects of salt stress on legumes.

Keywords Legumes · Salinity · Salt injury · Alleviation strategies · Molecular responses · Tolerance

Introduction

Grain legumes offer the main source of calories and proteins for a large proportion of the world's population due to their relatively cheap sources of dietary protein, vitamins

and minerals for humans and animals mostly in developing countries around the Mediterranean region (Jha et al. 2019). Legumes occupy 12–15% of arable land worldwide to produce 27% of major crop production (Mishra et al. 2014a, b).

Environmental abiotic stresses severely affect plant growth and productivity worldwide. In Mediterranean countries, salinity is considered one of the most important environmental stresses hampering legume growth and yield, particularly in semi-arid and arid regions (Hellal et al. 2012). Most legume plants are sensitive to high concentrations of salts in the soil. Salinity affects almost all aspects of plant development (Shrivastava and Kumar 2015). Salinity adversely affects plant growth by decreasing plant's ability to absorb water from soil along with the accumulation of toxic ions (Na^+ and Cl^-) in cell tissues (Dell'Aversana et al. 2021). The imposed osmotic and ionic stress occurring reduces cell expansion, hinders tissue growth leading to the reduction of grain yield and quality (Farooq et al. 2017, Dell'Aversana et al. 2021). Roots exposure to high chloride (Cl^- ions) triggers a long-distance signal resulting in leaf apoplastic pH alkalization, leaf Abscisic acid (ABA) redistribution, stomata closure and photosynthesis impairment (Geilfus 2018). The soil salinity also decreases nodulation, nodule

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weight, nitrogen fixation, nitrogenase activity, N content and nitrogen fixation (Cordovilla et al. 1994).

It is well established that salt stress alters plant growth and development by reducing nutrient uptake, which eventually affects cell function and alters cellular, biochemical and metabolic activities (Abid et al. 2017; Assaha et al. 2017). To cope with this, legumes have developed complex mechanisms to overcome the harmful effect of Na^+ on cells (Tester and Davenport 2003; Hassan et al. 2016).

Several strategies have been developed in order to improve legume growth under salinity stress and mitigate the toxic effect of salt at different stages of plant development (Ashraf and Akram 2009). Breeding for salt-tolerant genotypes and the identification of novel salinity tolerance loci can be an approach to alleviate the harmful effect of salt stress (Atieno et al. 2021). Genetic transformation technology offers the possibility to increase plant tolerance to salinity, through the genetic manipulation of genes known to be involved in plant response and/or tolerance to salt stress (Mishra et al. 2014a, b). Additionally, the combination of genetic engineering and traditional breeding tools appears to be more efficient for developing crops adapted to salt stress (Anwar and Kim 2020). The Plant Growth Promoting Bacteria (PGPB)-legume can be used as a cost-effective way to increase salinity tolerance and boost plant growth. Particularly, the Plant Growth Promoting Rhizobia (PGPR)-legumes symbiosis is naturally occurring and it contribute to salt stress tolerance (Wang et al. 2016a, b). AMF is another alternative that acts as growth regulator and mitigates the detrimental effects of salt stress on plants, as well as, enhancing plant growth and yield (Hashem et al. 2014). Whereas, the synergistic interactions of PGPR and AMF with legumes can multiply the ameliorative capacity under salinity stress (Nadeem et al. 2014). Salt stress can also be alleviated by the application of seed or plant priming (Azooz 2009; Dawood and El-Awadi 2015; Sagervanshi et al. 2021). In this review, we describe (1) the effect of salinity on legume growth and development, (2) the molecular responses to salt stress in legume plants and (3) the different strategies to alleviate salinity stress in this family. The tolerance mechanisms conferred by legumes' association with Rhizobium (Rhizobium-legume symbiosis) are also highlighted.

Adverse effects of salt stress on the growth and development of legumes

Effects of salt on legume seed germination

Seed germination is one of the most critical stages in seedling establishment, representing the first contact with the encountering environment, particularly water and soil (Tlahig et al. 2021). Numerous studies have reported reductions

in seed germination along with a delay in this process in legumes with increasing salinity levels (Sidari et al. 2008; Farissi et al. 2011; Bouallègue et al. 2017; Anaya et al. 2018; Tlahig et al. 2021). The impact of salt stress on seed's germination was highly variable depending on plant species (Table 1). High sodium chloride (NaCl) concentrations limit cell division and expansion, which obstruct seed germination and induce cell death (Keshavarzi 2011). Salt inhibition of seed germination is mainly attributed to the restriction of water uptake and ion toxicity on the embryo. This results in the obstruction of seed's reserves mobilization due to the inhibition of hydrolytic enzyme activities mainly α -amylase, β -amylase and α -glucosidase (Sidari et al. 2008; Farissi et al. 2011; Farooq et al. 2015). Other authors explained this inhibition as the suppression of ethylene production during imbibition. While others have linked it with the decrease in the gibberellin (GA) content due to the negative regulation of GA biogenesis pathway by salt stress along with the activation of ABA biosynthesis pathway. Consequently, this variation leads to a reduction in the GA/ ABA ratios showing that these two phytohormones are key determinants of seed germination (Meng et al. 2016; Shu et al. 2017; Chang et al. 2010).

Effects of salt on legume growth

It is well established that salt stress inhibits plant growth in many plant species, even in legumes' species (Luo et al. 2006). Salt induced growth arrest was reported in many Fabaceae plants. Pitann et al. (2011) have found that salt stress application induced a significant decrease in legume growth attributes. Similar findings were also underlined by Abdul Qados (2011). They reported that increasing NaCl negatively affected plant height, number of leaves and leaf area of faba bean cultivars. Deleterious effects of increased salinity have also been reported in pea and chickpea plants' growth and development (Yousef et al. 2020). In soybean, exposure to 150 mM of NaCl for 7 days resulted in the inhibition of plant growth (Ning et al. 2018). Mung bean (*Vigna radiata*) seedlings' growth inhibition in response to increased NaCl concentrations as been reported by Sehrawat et al. (2019). Bojović et al. (2010) explained the growth arrest by the disturbance of the ionic and osmotic balance caused by excessive salinity, which ultimately leads to plant destruction. Indeed, salt stress induces a decrease in soil water potential, disruption of nutrient uptake, disturbance of ionic balance and alteration of photosynthetic enzymes (Sheidaei et al. 2011; Saghari et al. 2020). Na^+ and Cl^- accumulation induced a decrease in photosynthesis and quantum yield due to chlorophyll degradation. The growth arrest due to salt stress can also be attributed to the lack of cell wall acidification (Pitann et al. 2011). The aforementioned structure is mediated by the activity of plasmalemma H^+ -ATPase

Table 1 Effect of salt stress on seed's germination of some legume's species

Plant species	Salt concentration	Reduction (%)	References
<i>Arachis hypogaea</i> L.	200 mM	45	Desheva et al. (2020)
<i>Acacia longifolia</i> subsp. <i>longifolia</i>	200 mM	80–85	Welgama et al. (2019)
<i>Centrosema pubescens</i>	16 dS/m	55	Sevanayak et al. (2020)
<i>Cicer arietinum</i>	7.47 g/L	≈ 87	Lavrenko et al. (2019)
<i>Clitoria ternatea</i>	16 dS/m	70	Sevanayak et al. (2020)
<i>Glycine max</i> L.	300 mM	70–80	Kumar (2017)
<i>Lathyrus odoratus</i> L.	21.6 dS/m	≈ 15	El-Serafy et al. (2021)
<i>Lotus ornithopodioides</i> L.	250 mM	20–44	Hajri et al. (2018)
<i>Macroptilium atropurpureum</i>	16 dS/m	35	Sevanayak et al. (2020)
<i>Macrotyloma uniflorum</i>	20 dS/m	≈ 25	Pantola et al. (2017)
<i>Medicago ciliaris</i> L.	200 mM	≈ 64–78	Mbarki et al. (2020)
<i>Medicago intertexta</i> L.	150–200 mM	97–98	Mbarki et al. (2020)
<i>Medicago sativa</i>	200–250 mM	50–79	Bicakci et al. (2018)
<i>Medicago scutellata</i> L.	150–200 mM	97	Mbarki et al. (2020)
<i>Phaseolus vulgaris</i> L.	85.5 M	42	Alsaeedi et al. (2017)
<i>Phaseolus vulgaris</i> L.	300 mM	40	Mansouri et al. (2019)
<i>Phaseolus vulgaris</i> L.	150 mM	12–34	Yu et al. (2019)
<i>Sulla coronaria</i> (L.)	150–200 mM	60–76	De Rossi et al. (2021)
<i>Trifolium rubens</i>	40 mM	80	Kotodziejek (2018)
<i>Vachellia karroo</i>	600 mM	100	Kheloufi et al. (2017)
<i>Vicia faba</i> L.	200 mM	55	Anaya et al. (2018)
<i>Vigna unguiculata</i> (L.) Walp	12 dS/m	15–40	Islam et al. (2019)
<i>Vigna unguiculata</i> (L.) Walp	250–300 mM	100	Osman et al. (2019)
<i>Vigna radiata</i> L.	15.6 dS/m	≈ 50	Dutta and Bera (2014)
<i>Vigna radiata</i> L.	160 mM	48–49	Podder et al. (2020)
<i>Vigna radiata</i> L.	150 mM	70	Ghanbari et al. (2020)

and cell-wall-loosening enzymes that stimulate plant growth by prompting cell growth and enlargement (Pitann et al. 2011). Therefore, the disturbance in this process decreases cell growth rate, which ultimately results in plant growth reduction (Pitann et al. 2011; Farooq et al. 2017).

Effects of salt on legume physiology

Plant exposure to salt stress triggers a wide range of physiological changes. Several studies have underlined the inhibitory effect of salt stress on biochemical processes, of which photosynthesis is the most important (Qados 2011). Salt stress alters photosynthetic pigments, which influence the photosynthesis activity (Garg and Singla 2004; Sheidaei et al. 2011; Hniličková et al. 2019; Nadeem et al. 2019; Najar et al. 2019; Saghari et al. 2020). Ahmad et al. (2018) explained the alteration in plant photosynthesis activity by Mg^{2+} uptake restriction and the alteration in photosynthetic pigments mostly chlorophyll by the activation of chlorophyllase enzymes. NaCl stress triggers the synthesis of reactive oxygen species (ROS) (superoxide, hydrogen peroxide, etc.), which are components of oxidative stress. However, the ROS over-accumulation harms

the chloroplast layers, inhibits Rubisco and leads to stomatal closure which ultimately result in a significant reduction in plant growth and productivity (Ahmad et al. 2017; Alzahrani et al. 2019b).

Photosynthesis impairment induced by osmotic stress that occurred as a result of salinity causes irreversible metabolic imbalances and prompts the synthesis of ROS (Geilfus et al. 2015). Normal concentration of ROS is required for cell signaling. However, their overproduction induces distinct changes in cell biochemistry in terms of membrane permeability. Indeed, ROS accumulation constrains cell metabolism through the stimulation of DNA, proteins and lipids oxidation which can cause serious damage to cellular processes such as lipid peroxidation, protein degradation, inactivation of enzymes, damage to nucleic acids, disruption in normal cell metabolism, and damage to cell membrane, which leads to cell death (Rohman et al. 2020; Sarker and Oba 2020). ROS accumulation has been reported in many legume species in response to salinity (Geilfus et al. 2015; El-Esawi et al. 2019). Hydrogen peroxide (H_2O_2) content subsequently increased in faba bean plants upon salinization (Geilfus et al. 2015). Alqarawi et al. (2014) explained this hazardous effect to the deleterious impacts of salt stress

on the composition of polyunsaturated fatty acids, which ultimately cause membrane dysfunction.

Effects of salt on legume yield

Salt stress inhibits legumes yield by 12–100% due to the alteration of plant morphological and physiological attributes (Farooq et al. 2017). A significant decrease in yield attributes namely the number of branches, the number of pods, the number of seeds per plant and the seed's yield was recorded in lentil (*Lens culinaris* Medik.) when cultivated in the presence of 100 mM of NaCl (Yasir et al. 2021). In faba bean, yield components including number of pods per plant, number of seeds per pod and seed weight was adversely affected by increasing concentrations of NaCl (Qados and Moftah 2015). Indeed, the number of pods, the number of seeds and seed weight decreased by 54%, 45% and 46% respectively when plants were grown in the presence of 200 mM of NaCl (Qados and Moftah 2015). This reduction is attributed to the negative effect of salt on pollen viability, stigma receptivity and photo-assimilates supply during reproductive stages (Farooq et al. 2017; Khan et al. 2017). The exposure to salinity causes ovarian disruption and injuries which lead to premature fruit drop and yield decrease as reported in Mungbean (*V. radiata*) (HanumanthaRao et al. 2016).

Salt stress adversely affects grain legume composition and quality. Salt stress significantly reduces protein content, carbohydrate and polysaccharide. The decrease in carbohydrate and polysaccharide contents is mainly attributed to ion toxicity, reduced photosynthesis and nutritional imbalance while the reduction in protein content is the result of the decline in nitrogen supply for soil (Swaraj and Bishnoi 1999; Qados 2011).

Effects of salt on biological nitrogen fixation

Symbiotic nitrogen fixation by rhizobia bacteria provides a source of biologically available nitrogen to legume plants (Vance et al. 2015). However, salt stress obstructs nodule formation and, therefore, the nitrogen fixation process (Bruning and Rozema 2013). It was previously reported that faba bean irrigation with 35% sea water inhibits nodule formation (Fahmi et al. 2011). This decrease was estimated to be 50% in *Lotus japonicus* cultivated in the presence of 50 mM NaCl (López et al. 2008). Similar inhibition rates have been recorded by Fahmi et al. (2011) in salt stressed faba bean plants. Katejri et al. (2003) have estimated the decline of nitrogen fixation in the same species under saline conditions by 16–24%. In *Medicago truncatula*, the reduction in nitrogen fixation rate was less pronounced (14% at 50 mM NaCl) (López et al. 2008). Manchanda and Garg (2008) explained this phenomenon by root hair formation

obstruction due to salt stress injuries which ultimately reduce the nodule's number per plant and the amount of fixed nitrogen per unit of nodules. Furthermore, root-hair curling, a main step in rhizobia colonization was negatively impacted by NaCl-induced stress (Zahran and Sprent 1986).

Salt stress disturbs nitrogenase activity, the key enzyme involved in atmospheric N₂ fixation by Rhizobia strains. Furthermore, the total as well as specific nitrogenase activity of root nodules decreases with salinity stress (Yousef and Sprent 1983; Fernández-Pascual et al. 1996). Nevertheless, glutamine synthetase and glutamate synthase, which are required for ammonium assimilation display a different tolerance pattern in salt stress conditions (Bernard and Habash 2009; Betti et al. 2012). It was reported that glutamine synthetase is more resistant to salinity than glutamate synthase, which ultimately reduces the assimilation of ammonium under saline conditions (Cordovilla et al. 1999).

The set of symbiotic interaction relies on the activation of a sequence of events coordinated by the host plant and the symbiotic rhizobia (Zhang et al. 2019). The signaling process starts with the exudation of flavonoids from the leguminous roots, which stimulates the secretion of lipo-chito oligosaccharides nodulation factors (NOD). The NOD is defined as the fundamental molecular signal that trigger the nodulation program (Bruning and Rozema 2013). However, salt stress adversely affects the signal exchange. Furthermore, salt stress increases the biosynthesis of nod factors (NFs) and induces changes in their structures as previously reported by Hasanuzzaman et al. (2020). These newly generated NFs induce morphological and biochemical changes namely, root hair deformation, intra-and extra-cellular alkalization, ROS accumulation, phosphatidic acid and diacylglycerol formation (Hasanuzzaman et al. 2020). The root hair deformation has an inhibitive action on rhizobia colonization, which ultimately reduces the infection rate, weight and number of nodules (Egamberdieva et al. 2014).

The harsh effects of salt stress on plant growth, physiology, productivity, and nitrogen fixation are the direct result of the modification of molecular machinery. Thus, the thorough understanding of plant stress response mechanisms will provide valuable information for improving crop engineering for salt stress tolerance.

Molecular responses to salt stress in legume plants

Legumes' genetic response to salt

Salt stress affects plants in multiple ways: (1) osmotic injury due to high concentrations of solutes which ultimately leads to a water deficit; (2) ionic stress as a result of the disturbance of K⁺/Na⁺ contents and (3) nutritional disorders,

which arise from the availability, absorption and transport of nutrients within the plant (Assaha et al. 2017). In response to these harmful conditions, legumes evolve complexed mechanisms to mitigate the deleterious effects of stress and ensure plant survival under these harmful conditions. These mechanisms aim to lower the toxic effect of Na^+ and preserve a low cytosolic Na^+ concentration along with a high K^+/Na^+ ratio by reducing Na^+ influx into root cells, Na^+ compartmentation into vacuoles and Na^+ exclusion from root cells (Tester and Davenport 2003; Hassan et al. 2016).

Salt stress sensing and signal transduction in legumes

The high amounts of Na^+ detected in soil under salt stress conditions modify the electrochemical gradient which prompts Na^+ influx from the soil into root cells (Blumwald et al. 2000). Na^+ entry occurs via the symplastic and apoplastic pathways (Isayenkov and Maathuis 2019). The apoplastic pathway (through cell walls) which represents only 1% of the transpirational volume flow, is described in the literature as a direct and continuous flow from the outside of the root cell to the xylem (Kronzucker and Britto 2011; Hossain et al. 2016). In faba bean, it has been demonstrated that short term exposure to NaCl concentrations enhanced Na^+ uptake through the apoplastic pathway, which strongly underlines the importance of this transport route in Na^+

uptake and signaling in salt stressed beans (Shahzad et al. 2013). In turn, the root endodermis interrupts the apoplastic transport of Na^+ ions due to the deposition of hydrophobic compounds (lignin and suberin). It thus allows the formation of the framework of the Casparian strip, which constitutes a physical barrier for water and ion movement. At this level, ions and water are forced to undergo membrane control and to take the symplastic path (Ketehouli et al. 2019) (Fig. 1).

The Na^+ root uptake through the symplastic pathway requires the intervention of specific transporters (Kronzucker and Britto 2011). Initial entrance of Na^+ ions into the cytoplasm of root cortical cells mainly occurs either via non-selective voltage-dependent cation channels (NSCCs) or through the intervention of sodium transporters (Demidchik and Maathuis 2007). Nonselective cation channels (NSCCs) are encoded by two gene families: glutamate receptor-like channels (GLRs) and cyclic nucleotide-gated channels (CNGCs) (Zhang et al. 2002). Several studies have shown that DA-NSCCs (Depolarization-activated nonselective cation channel) transporters are involved in K^+ loading into xylem and its redistribution in *Phaseolus vulgare* plants (Zhang et al. 2004; Yang et al. 2005). Na^+ influx into cells induces membrane depolarization, which instigate the K^+ leak through the intervention of depolarization-activated K^+ -selective outwardly rectifying KOR channels. Na^+ entry and accumulation in the cytosol prompted ROS production

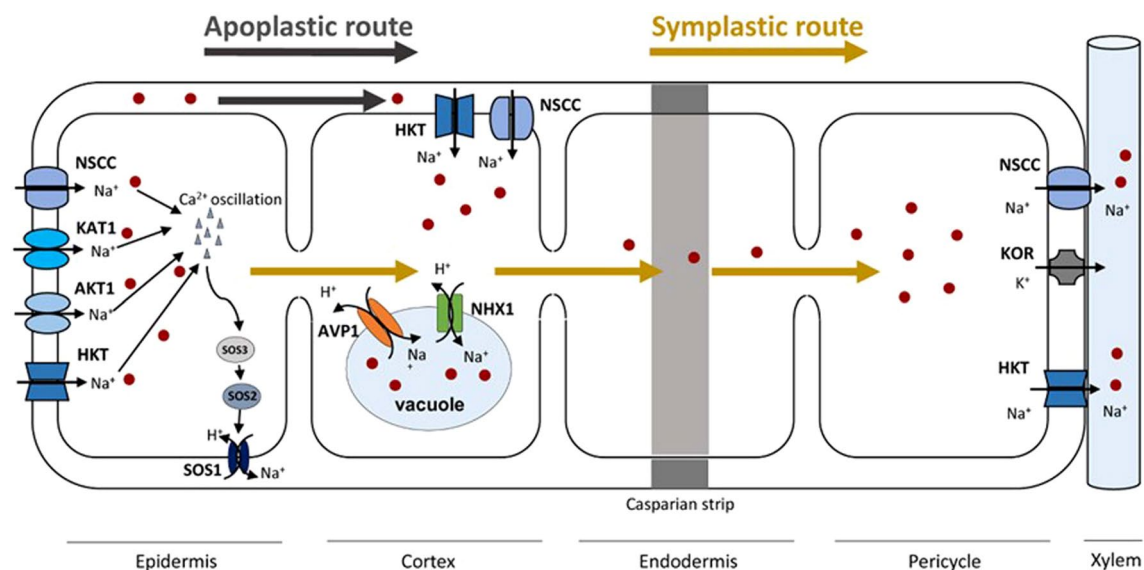


Fig. 1 General mechanism of Na^+ entry into root cells of legume plants. Na^+ toxic ions enter to root cell through apoplastic or symplastic paths. The apoplastic route (grey narrow) occurs as a direct and continuous flow from the outside of root cell to the xylem. Within this route, Na^+ transport is interrupted in the endodermis by the casparian strip. The symplastic pathway is mainly operated through transporters. Within the latter path, Na^+ absorption by epidermis cells is promoted by Nonselective Cation Channels (NSCCs), High Affinity Potassium Transporters (HKT) proteins and the Shaker Type K^+

channels: AKT1 and KAT1. Na^+ influx cause membrane depolarization, Ca^{2+} activation and the generation of Ca^{2+} oscillations that serve as a second messenger that activate SOS pathway that trigger Na^+ exclusion to the apoplast. Apoplastic Na^+ ions reach the cortex through the following transporters: NSCC and HKT. At this level, Na^+ ions can be stocked in vacuoles promoted by NHX1 and AVP1 transporters. Non sequestered ions reach the xylem trough NSCC and HKT transporters

which can lead to the activation of NSCC channels providing an additional avenue for further K^+ leakage (Percey et al. 2014). Other transporters like the High Affinity Potassium Transporters (HKT) proteins and the Shaker Type K^+ channels (AKT1 and KAT1), have been described to be involved in Na^+ uptake in many plant species, including *Arabidopsis thaliana*, *Oryza sativa* and the halophyte *Suaeda maritima* (Kader and Lindberg 2005; Wang et al. 2007; Horie et al. 2009). However, no previous work had demonstrated their presence in legume plants and their implication in sodium transport or salt stress signaling.

The pronounced increase of cytoplasmic Na^+ occurring because of Na^+ influx disturbs the enzymatic functions of plant cells. Na^+ internal concentration can be reduced mainly through three distinctive processes that enable: (1) reduction if Na^+ entry into cells; (2) trigger of Na^+ compartmentation into cell vacuoles and (3) stimulation of Na^+ efflux out of cells (Ji et al. 2013). The NSCCs-orchestrated influx of Na^+ ions causes membrane depolarization, Ca^{2+} activation and the generation of Ca^{2+} oscillations and a stress signal (Tester and Davenport 2003). The Ca^{2+} -generated signal serves as a second messenger and activates specific transporters and channels involved in sodium extrusion. This signal is perceived by SOS3 (Salt Overly Sensitive 3), a sensor protein that interacts with the serine/threonine protein kinase SOS2 (Manchanda and Garg 2008). This interaction causes the phosphorylation of the plasma membrane Na^+/H^+ exchanger SOS1, known for its involvement in Na^+ retrieval from cells. In roots, about 70–95% of the Na^+ ions entering in the roots via the symplastic route are extruded to the apoplast (Tester and Davenport 2003). The SOS1 mechanism of Na^+ efflux from roots and its loading into xylem has been intensively studied in *Arabidopsis* (Shi et al. 2002). SOS homologs had been identified in many plant species including legumes (Liu et al. 2015a; Quan et al. 2016). SOS1 and SOS2 gene transcripts increased substantially and subsequently in salt stressed alfalfa (*Medicago sativa*) genotypes (Quan et al. 2016). SOS1 expression was significantly induced after 2 days of salt stress exposure which contribute to Na^+ extrusion in soybean (*Glycine max*) S111-9 genotype (He et al. 2015). In salt-tolerant *Medicago falcata*, SOS1 expression was upregulated in response to salt stress. This salt-enhanced tolerance was correlated with the higher expression of the SOS1 gene, required for more efficient Na^+ retrieval from root cells (Liu et al. 2015a).

Sodium vacuolar compartmentation is considered one of the key strategies used by plants against salinity (Yang et al. 2005). It allows the removal of potentially toxic Na^+ ions from the cytoplasm and cellular osmolarity increase, which are required for a better tolerance to osmotic stress (Ahmad and Rasool 2014). Sodium/hydrogen exchanger (NHX) proteins, which belong to the Na^+/H^+ antiporter family of transporters, play a crucial role in salt tolerance

in many plant species through prompting Na^+ accumulation in vacuoles and pH regulation (Zahran et al. 2007). A number of genes encoding vacuolar Na^+/H^+ antiporters have been isolated from diverse legume plants including VrNHX1 from mung bean (Mishra et al. 2014b), TrNHX1 from *Trifolium repens* and MtNHX1 and its ortholog' from *Medicago truncatula* (Al-Farsi et al. 2020). In legume plants, several reports have stated the involvement of the NHX gene family in plant response to salt (Tang et al. 2010; Mishra et al. 2014b; Quan et al. 2016). For instance, it has been found that *MsNHX1*, an Na^+/H^+ antiporter of *M. sativa*, was highly expressed in leaf tissue under salt stress, underlying its putative role in Na^+ compartmentation in leaf vacuoles (Yang et al. 2005). The constitutive expression of *AtNHX1* in soybean (*G. max*) confers a better tolerance to salt stress by prompting the accumulation of high amounts of toxic Na^+ ions (Li et al. 2010). Similar findings were also reported in the model legume *Lotus corniculatus*, in which the soybean *NHX1* gene was overexpressed (Sun et al. 2006). In mung bean, the increased salt tolerance was correlated with a higher K^+/Na^+ ratio in the aerial parts through the accumulation of high amounts of Na^+ ions in roots, which is considered an efficient strategy of salt tolerance through the restriction of Na^+ movement in roots (Mishra et al. 2014b).

The tonoplast H^+ -pyrophosphatases are H^+ pumps that allowed the acidification of vacuoles through pyrophosphate hydrolysis and orchestrate the active proton transport (Segami et al. 2014). They ensure the generation of H^+ motive force required for ion entry into vacuoles and thus the regulation of cell turgor (Bao et al. 2016). Genetic manipulation of H^+ -pyrophosphatases in many plant species including legumes conferred a better tolerance to salt as a result of increased Na^+ accumulation in leaves and roots (Bao et al. 2009; Jha et al. 2013; Bassil and Blumwald 2014). The co-expression of *Zygophyllum xanthoxylum* *ZxVPI-1* and *ZxNHX* genes in alfalfa (*M. sativa*) resulted in a significant accumulation of Na^+ in leaves and roots. Transgenic alfalfa plants also showed less injury from NaCl-induced stress, which ultimately conferred a better tolerance to salt (Bao et al. 2016). The overexpression of the *AtAVPI* gene in transgenic alfalfa plants exhibited high Na^+ amounts, which was likely related to the enhanced transport efficiency of the vacuolar Na^+/H^+ antiporter resulting from the overexpression of the *AtAVPI* gene (Bao et al. 2009). In soybean, co-expression of both *A. thaliana* *AtNHX1* and *AtAVPI* genes confers better salt tolerance to transgenic plants. This increased tolerance to salt was mainly assessed due to the ability of transgenic plants to sequester toxic Na^+ ions in their vacuoles as a result of the activity of both NHX1 and AVPI transporters (Nguyen et al. 2019a) (Fig. 1).

Transcriptional regulation of salt responsive genes in legumes

Transcription Factors (TFs) play key roles in the transcriptional regulation of plant responses to salinity and other abiotic stresses. Many transcription factors involved in the salt stress response had been identified (Fig. 2). The most studied ones are Zinc Finger Proteins (ZFPs), AP2/EREBP (APETALA2/Ethylene-Responsive Element Binding Proteins), NAC TFs, bZIP (basic leucine zipper domain) and WRKYs family of TFs, which are involved in plant response to salt stress. The overexpression of genes encoding for these TFs confers a better tolerance to salt stress. The expression of ZFP protein was highly up-regulated in alfalfa plants when subjected to salt stress (Chao et al. 2009).

The AP2/ERF are TFs belonging to the superfamily of AP2/EREBP regulate the transcription of target genes through direct interaction with dehydration responsive elements found at the promoters of target genes and instigate salt stress response (Sakuma et al. 2006). The expression of AP2/EREBP subfamily members were significantly induced by salt in legume plants (Li et al. 2005; Pennycooke et al. 2008). The CCAAT motif-binding factor (CBF) gene expression was significantly regulated by salt stress in soybean (Li et al. 2005). Ethylene-responsive transcription factor (ERF-WIN1), which also belongs to the AP2/EREBP subfamily has been reported to be highly induced in response to salt and osmotic stress in chickpea (Kaashyap et al. 2018). In *M. sativa*, the expression of *CBF4* gene was highly induced in salt tolerant genotype in response to high NaCl concentrations, which might explain the increased tolerance observed in this genotype. The overexpression of *Medicago truncatula* CBF4 enhanced plant tolerance to salt stress in transgenic plants by regulating the expression of downstream genes (Li et al. 2011a). Li et al. (2011a) identified two of the *MtCBF4* regulated genes; *MtCAS15* (cold acclimation-specific 15) and *MtCAS31* (cold acclimation-specific 31), encoding for dehydrin proteins. *MtCAS31* was later proposed as a key actor in the autophagic degradation pathway. Li et al. (2020) have demonstrated that *MtCAS31* interacts with the plasma-membrane intrinsic protein *MtPIP2;7*, a plant aquaporin protein, and induces the degradation of this latter. In *Cicer*

arietinum, the dehydration responsive element (DRE/CRT) showed differential expression in the salt-tolerant genotype in comparison with the sensitive genotype (Kaashyap et al. 2018).

Another important transcription factors family that has been widely associated with salt tolerance in legumes such as soybean (*G. max*) and peanut (*Arachis hypogaea*) is the NAC family. In peanut, several NAC genes were differentially expressed in response to salt which strongly suggests that these TFs are involved in the response to salt (Yuan et al. 2020). In chickpea, RNAseq analysis revealed that the expression of many NAC genes was significantly up-regulated in the salt-tolerant genotype (Kaashyap et al. 2018). In soybean, the overexpression of *GmNAC06* enhanced plant tolerance to NaCl excess, by controlling the K^+/Na^+ ratio prompting proline and glycine betaine accumulation in transgenic plants (Li et al. 2021). The introduction of *OoNAC72*, a NAC-Type *Oxytropis ochrocephala* transcription factor in *A. thaliana*, increased transgenic plants tolerance to salt and drought. This enhanced resistance was correlated with the up-regulation of the expression of many stress-responsive genes (*RD29A*, *RD29B*, *RD26*, *LEA14*, *ANACPR19*, *ZAT10*, *PP2CA* and *NCED3*), suggesting that this transcription factor regulates the expression of these genes (Guan et al. 2019). Constitutive expression of chickpea *CarNAC4* in *A. thaliana* enhanced salt tolerance in transgenic plants (Yu et al. 2016). *CarNAC4* overexpression enhanced the expression of stress-responsive genes, including *RD29A*, *ERD10*, *COR15A*, *COR47*, *KIN1* and *DREB2A* which clearly indicated the involvement of *CarNAC4* as a transcription factor regulating salt-related genes.

The basic leucine zipper (bZIP) family of TFs is involved in many aspects of plant development and interaction with environment. They regulate gene expression by interacting with specific cis-elements that include the ABRE (ABA-responsive element) (Ayra et al. 2018). Previous reports had demonstrated the responsiveness of *bZIP* genes to salt stress in legume species such as common bean (*Phaseolus vulgaris*), soybean (*G. max*) and luserne (*Medicago truncatula*) (Liao et al. 2008; Hiz et al. 2014; Wang et al. 2015a). In *P. vulgaris*, many *bZIP* genes displayed a differential expression in response to salt excess. The authors also suggested

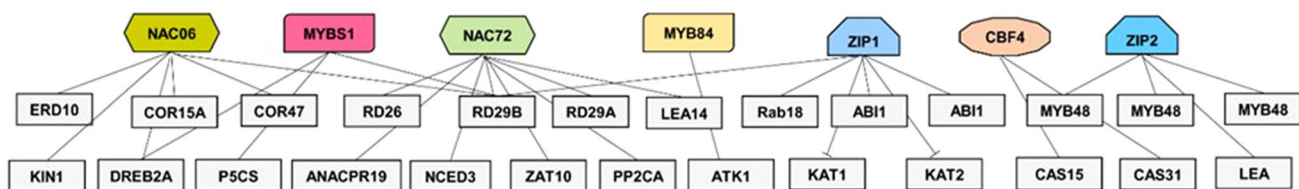


Fig. 2 A schematic representation of the transcriptional regulatory network involved in the transcriptional regulation of salt responsive genes in legume plants. Salt-responsive genes (symbolized by grey

boxes) can be regulated by one or several transcription factors (represented in colored box) which underline the complexity of the molecular response of legume species to salt stress

that *PvZIP* genes are key regulators that interact with other TFs to control the expression of stress-responsive genes in common bean (Ayra et al. 2018). The soybean *GmbZIP2* expression was significantly up-regulated in salt stressed plants and triggered the expression of several stress response genes required for ion homeostasis, ROS scavenging or scaffolding molecule that ensure protein proper functioning (Yang et al. 2020). Among the regulated genes, the authors identified the following genes: *GmMYB48*, *GmWD40*, *GmDHN15*, *GmGST1* and *GmLEA*. Another member of the bZIP transcriptional regulator family; *GmbZIP1* was found to be involved in the set of stress responses in soybean. For instance, Gao et al. (2011) have demonstrated that the overexpression of *GmbZIP1* conferred multiple stress tolerance mainly to salt, drought and cold. This increased tolerance was linked to the regulation of ABA-stress regulated target genes, namely abscisic acid insensitive 1 and 2 (*ABI1* and *ABI2*), Desiccation-Responsive *RD29B*, and rab-related (responsive to ABA) *Rab18* genes. The *GmbZIP1* factor was also reported as a negative regulator of stomatal closure by controlling the expression of *KAT1* and *KAT2* which encode for inward-rectifying K^+ channel subunits, involved in stomatal aperture (Kim et al. 2004; Gao et al. 2011).

The WRKY transcription factors play a main role in the transcriptional regulation during legume response to salt stress. *WRKY72* and *WRKY73* were differentially expressed in salt tolerant genotype of chickpea. Thus, these two TFs were proposed as key actors in chickpea tolerance to salt stress (Kaashyap et al. 2018). The expression of *MsWRKY11* was highly up regulated in alfalfa plants suffering from salt stress injuries. The overexpression of this TF in soybean enhanced transgenic plants tolerance and improved plant physiological attributes under salt stress conditions. This increased tolerance was linked to the accumulation of proline and the activation of ROS scavenging enzymes (Wang et al. 2018a). Similar findings were also recorded in *A. thaliana* overexpressing the *G. max GmWRKY54* gene (Zhou et al. 2008).

Another family of transcriptional regulators that seems to be involved in legumes response to salinity is the MYB (v-myb avian myeloblastosis viral oncogene homolog) family. The expression of *MtMYBS1* gene is inducible by NaCl (Dong et al. 2017). Its introduction in *A. thaliana* enabled the transgenic plants to overcome salt stress through the regulation of the expression of *P5CS*, a key gene involved in the proline biosynthesis pathway (Dong et al. 2017). The constitutive expression of *M. sativa MsMYB4* in *A. thaliana* improved the plants' salinity tolerance in an ABA-dependent manner (Dong et al. 2018). In soybean, *GmMYB84* gene was highly induced in salt stressed plants. The heterologous expression of the *GmMYB84*-encoding gene in *A. thaliana* confers a better tolerance to salt stress through a direct interaction with the promoter of *GmATK1*, the homolog of

Arabidopsis K⁺ Transporter 1 (AKT1) involved in K^+ acquisition and homeostasis under saline conditions (Zhang et al. 2020). Constitutive expression of *M. truncaluta MYBS1* in *A. thaliana* unraveled a positive regulation of the expression of salt stress responsive genes mainly, *RD22*, *RD29A*, *RD29B*, *P5CS*, and *DREB2A* under saline conditions (Dong et al. 2017). The up-regulated genes are associated with proline biosynthesis (*P5CS*), Dehydration-Responsive proteins (*DREB2A*, *MYB2*) and Desiccation-Responsive proteins (*RD22*, *RD29A* and *RD29B*).

Expression of salt stress responsive genes

To prevent stress damages and repair stress-induced injuries, plants have evolved several pathways to ensure cell survival even at metabolically inhibitory levels of ionic and osmotic stresses. These pathways mainly include ion homeostasis (Na^+ exclusion and Na^+ sequestration), osmolytes accumulation, induction of proteins involved in stress responses, and restoration of osmotic balance (Manchanda and Garg 2008). The induction of stress proteins, more likely Late Embryogenesis Abundant (LEA), and Heat Shock Protein (HSP) families, and their involvement in legumes' response to salt excess will be discussed in this sub-section.

LEA (Late Embryogenesis Abundant) proteins are members of a large group of hydrophilic, glycine-rich proteins found in a wide range of plant species (Magwanga et al. 2018). LEA proteins had been studied in soybean plants exposed to abiotic stresses (Phang et al. 2008). It was previously reported that the constitutive expression of either Soybean *PM11* or *PM30* in *E. coli* enabled the transgenic bacteria to grow in saline growth conditions which strongly suggests that these genes play an important role in soybean tolerance to salinity (Lan et al. 2005). In *M. truncatula*, salt stress induced the accumulation of transcripts from LEA genes belonging to groups 2, 3, 4, 6 and 7 (Battaglia and Covarrubias 2013). The overexpression of *G. max GmLEA2-A* in transgenic *Arabidopsis* conferred tolerance to salt stress suggesting that this gene is a key actor in plant response to salt (Wang et al. 2018a, b).

Another family of stress proteins that plays a crucial role in legumes' response to salt excess is the HSP family. HSPs are involved in refolding misfolded proteins and degrading damaged proteins under stress conditions (Zhou et al. 2013). Büyük et al. (2016) showed that *PvHSP70* was inducible by salt stress in common bean (*P. vulgaris*). Other HSPs proteins have been reported as involved in *P. vulgaris* response to salt stress. This is the case of *PvHSP90* and *PvDnaJ3*, whose expression was significantly regulated in salt stressed plants (Hernández-Lucero et al. 2014). The expression of *GmHsp90A2*, *GmHsp90A4*, *GmHsp90B1*, *GmHsp90C1.1* and *GmHsp90C2.1* was highly induced by salt stress in *G. max*. Their overexpression in *A. thaliana* conferred increased

tolerance to salinity by minimizing the deleterious effects of salt (Xu et al. 2013).

Epigenetic regulation of legumes' response to salt

Epigenetic regulation of gene expression plays a crucial role in plant response to salinity. This regulatory process, operates through different mechanisms involving DNA methylation, histone modifications and non-coding RNA that induce gene activation or knock out (Salgotra and Gupta 2019).

DNA methylation

DNA methylation is the foremost epigenetic mode of regulation observed in eukaryotes. This process can be simply defined as the addition of a methyl group on C5 of the cytosine base to form 5-methylcytosine (Salgotra and Gupta 2019). Plant DNA methylation is found in three different contexts; CG, CHH and CHG, wherein H can be any base except for guanine (Windels et al. 2021). In plants, DNA methylation is basically catalyzed by a group of methyltransferase enzymes (Al-Lawati et al. 2016). DNA methylation is usually associated with gene silencing, whereas DNA demethylation allows gene activation (Salgotra and Gupta 2019). In pigeon pea, salinity induced a global decrease of DNA methylation, while 26% increase in global DNA methylation has been recorded in alfalfa (*M. truncatula*) plants irrigated with 20 dS/m (Al-Lawati et al. 2016; Awana et al. 2019). Under salt stress conditions, a positive correlation was demonstrated between global DNA methylation and methyltransferase genes transcripts. The authors also underlined the preponderant role of DNA methylation in salt tolerance acquisition in alfalfa by applying a DNA methylation inhibitor that increased plant susceptibility to salt (Al-Lawati et al. 2016). Soybean exposure to salt enhanced global DNA demethylation mainly in salt tolerant genotype. Profound demethylation analysis showed that CG and CHG contexts were more critical than CHH in gene regulation of soybean adaptability to salinity (Liang et al. 2019). This increase was positively correlated with an increase in DNA demethylases transcripts (Al-Lawati et al. 2016). Van Dam et al. (2009) suggested that the high incidence of the DNA demethylation process under stressful conditions could be linked to the role of chromatin demethylation as a transcriptional switch for several stress-regulated genes. In soybean salt-tolerant genotype, some differentially methylated genes are involved in gene transcription, DNA repair, RNA splicing, protein processing in the endoplasmic reticulum processes (Liang et al. 2019). Overall, the epigenetic changes occurring at the DNA methylation level appears to be a key regulatory process in plant response to salt stress. This epigenetic process of regulation can occur either through demethylation or methylation depending on plant species and stress period.

Non-coding RNAs

Non-coding RNAs (ncRNAs) are functional RNAs with low-protein coding potential. They can be classified according to their length into small ncRNAs (sRNAs) (18–30 nucleotides), medium-sized ncRNAs (31–200 nucleotides) and long non-coding RNAs (LncRNAs) (more than 200 nucleotides) (Wang et al. 2017). microRNAs (miRNAs) are usually 21–23 nucleotides sRNAs deriving from intergenic regions and produced from single-stranded primary miRNAs (Bartel 2004; Alzahrani et al. 2019a). With a unique hairpin structure, they are known for their interaction with messenger RNAs (mRNAs) 3' untranslated regions (3'UTRs), which results in the down-regulation of target genes (Windels et al. 2021). miRNAs have recently emerged as a key regulator of gene expression at the transcriptional and post-transcriptional levels (Long et al. 2015). To date, with the development of high-throughput sequencing technology, a great number of small RNAs have been discovered in many plant species including legumes, particularly, *Medicago truncatula* and *Medicago sativa* (Lelandais-Brière et al. 2009; Long et al. 2015). Lelandais et al. (2009) have identified several salt responsive miRNAs in *M. truncatula* roots using a high-throughput sequencing strategy. Among the regulated miRNAs, miR393 expression was significantly repressed in *M. truncatula* salt stressed roots (Long et al. 2015). miR393 is involved in the regulation of auxin signaling pathway actors: Transport Inhibitor Receptor 1 (TIR1) and Auxin-related F-Box 2 (AFB2) and F-box protein genes encoding for auxin receptors, which underlines the role of miR393 in response to salt stress through the regulation of auxin action (Sunkar et al. 2007). In *Cicer aestivum*, three miRNAs were found to be upregulated in response to salt stress. This is the case of miR156, miR396 and miR319 (Kohli et al. 2014). Those miRNAs were reported to be involved in *Arabidopsis* response to high salinity (Liu et al. 2008). Three novel legume-specific miRNAs, miR008, miR015 and miR015 were also identified by the same authors through high-throughput sequencing. Evaluating their expression by Real-Time-PCR revealed their high responsiveness to salt stress which strongly supports their involvement in salt stress response in chickpea (Kohli et al. 2014). Target prediction of miRNAs targets revealed that miR156 is involved in the regulation of squamosa promoter-binding protein; a transcriptional activator (Williams et al. 2005; Preston and Hileman 2013). miR159 target encodes for a key enzyme involved in ester biosynthesis named acyltransferase, while miR319 and miR396 can be involved in the regulation of serine/threonine protein kinases and Mitogen Activated Protein Kinase (MAPK) protein, known for their involvement in salt stress signaling pathways (Kohli et al. 2014). Jatan et al. (2019) found that seven distinctive miRNAs were differentially expressed in chickpea in response to salinity.

Interestingly, they displayed different expression patterns. For instance, miR160, miR166, miR169, miR396, miR167 and miR171 expression was notably downregulated by opposition to miR159, whose expression was significantly induced. The regulated miRNAs mostly targeted transcriptional factors. Other miRNAs displaying a differential expression in response to high salinity have been identified in Chickpea by Khandal et al. (2017). This was the case for miR397, miR398 and miR164 whose expression was highly induced in chickpea salt stressed roots, while the expression level of miR399 was downregulated (Khandal et al. 2017). Throughout studying soybean roots response to salt stress, Sun et al. (2016) identified a total of 71 miRNAs candidates, of which 46 were responsive to salt stress. Among the regulated miRNA, miR399 was suggested to be involved in soybean root development and plasticity. Comparative expression analysis of miRNA in salt-tolerant genotype of faba bean (*Vicia faba*) revealed the responsiveness of 665 known miRNAs belonging to 31 miRNA families and 28 novel miRNA families. The expression pattern of most regulated miRNAs was downregulated. Target prediction showed that the regulated miRNAs modulate the expression of salt stress-related genes, namely those involved in plant hormone signal transduction, flavonoid biosynthesis, ATP Binding Cassette (ABC) transporter activity, ubiquitin-mediated proteolysis, flavonoid biosynthesis and DNA repair (Alzahrani et al. 2019a).

Besides miRNAs, other non-coding RNAs, known as long non-coding RNAs or lncRNAs are also involved in salt stress response. Lacking of protein-coding capacity, lncRNAs are typically about 200 nucleotides long and mainly located in the cytoplasm, with crapped 5'-ends and merged introns as well as poly(A) tails (Chen et al. 2019). Recent studies have underlined the importance of these non-coding RNAs in salt stress response in legumes including soybean (*Glycine max.*), groundnut (*A. hypogaea*) and *Medicago truncatula* (Wang et al. 2015a, b, c; Chen et al. 2019; Tian et al. 2020). For instance, soybean strand-specific transcriptome sequencing analysis allowed the identification of over 3030 lncRNAs in salt-stressed roots (Chen et al. 2019). In *M. truncatula*, Wang et al. (2015a, b, c) discovered that lncRNAs regulate *Medicago's* response to salt stress through the alleviation of ROS-induced oxidative stress. Within the same work, the authors discovered the function of several lncRNAs in salt stress response. Among the regulated lncRNAs, a functional analysis was conducted for TCONS_00116877, a lncRNA targeting the glutathione peroxidase-encoding gene (Medtr7g094600) (Wang et al. 2015a, b, c). Besides targeting genes involved in ROS scavenging, differentially expressed lncRNAs from chickpea (*C. arietinum*) act as regulators of several salt responses related genes, namely potassium transporter family genes, Tonoplast Intrinsic Protein (TIP) and PIP aquaporin-encoding genes,

serine/threonine-protein kinase and several transcriptional regulators (AP2, bZIP, MYB, WRKY, and NAC) (Kumar et al. 2021).

Histone modifications

Post translational regulation of histones alters the expression of genes by inducing chromatin restructuring or regulatory protein recruitment. Histone-occurring modifications can be the result of acetylation, methylation, ubiquitination, phosphorylation and succinylation reactions, etc. (Hashiguchi and Komatsu 2016; Yung et al. 2021). This process has been previously described for many plant species including *A. thaliana*, *O. sativa*, *Brassica napus* and *Solanum lycopersicum*. However, to our knowledge, histone methylation has not yet been studied in legumes.

Tolerance mechanisms in the *Rhizobium*-legume symbiosis

Rhizobium has a positive effect on legume subjected to salt stress by improving the activity of several molecules responsible for salt tolerance. Rhizobia synthesize 1-aminocyclopropane-1-carboxylase (ACC) deaminase, produce They synthesize ACC deaminase and produce various types of phytohormones and secondary compounds such as exopolysaccharides and regulate plant defense systems by activating plant's antioxidative enzymes (Fig. 3). ACC synthase and ACC oxidase transcripts increase under salt stress conditions leading to an increase in ethylene production in plants. The rhizobia have mechanisms that regulate plant ACC and, consequently, ethylene levels ACC deaminase (Okazaki et al. 2004), which is the key to bacterial plant growth-promotion. The ACC deaminase cleaves ACC, the immediate precursor of ethylene in plants, to form ammonia and α -ketobutyrate (Glick et al. 2007). This multimeric enzyme belongs to the tryptophan synthase (beta superfamily) of pyridoxal phosphate-binding proteins (Nascimento et al. 2016). The gene *AcdS* encodes the ACC deaminase under the transcriptional control of the regulatory gene *acdR* which encodes a Leucine-responsive Regulatory Protein (LRP)-like protein. The *acdR* is a common regulator of *acdS* gene transcription and is present in most strain possessing the *acdS* gene (including *Azorhizobium*, *Bradyrhizobium*, *Methylobacterium*, *Rhizobium*, *Sinorhizobium*, *Burkholderia*, and *Cupriavidus*) (Nascimento et al. 2014). For example, the *R. leguminosarum* *acdR* gene deletion resulted in a loss of ACC deaminase activity (Ma et al 2003), indicating that *acdR* is the main gene controlling *acdS* transcription in *R. leguminosarum*. The ACC deaminase has a crucial role in symbiotic conditions. The expression of exogenous ACC deaminase from *Rhizobia* species increased the ability to nodulate in several plant legumes such as *Medicago sativa* (Ma et al. 2004),

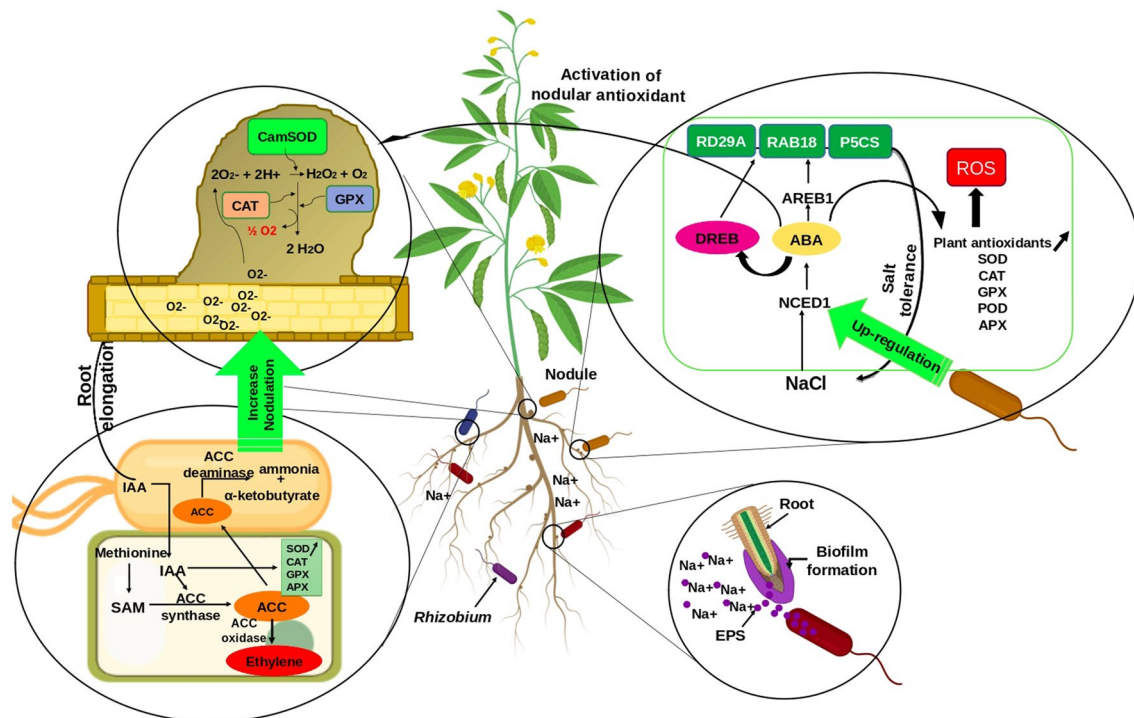


Fig. 3 Illustration of *Rhizobium* sp. molecular actions leading to legume tolerance and growth promotion under salinity stress. *Rhizobium* strains have the ability to synthesize ACC deaminase, phytohormones (e.g. IAA) and secondary metabolites (e.g. exopolysaccharides)

which can reduce the deleterious effects of salt stress and activate plant defense mechanisms through the activation of plant's antioxidative enzymes

Cicer arietinum (Brígido et al. 2013), *Medicago lupulina* (Kong et al. 2015), *Pisum sativum* (Ma et al 2003) and *Lotus* spp. (Conforte et al. 2010) under stress conditions. Brígido et al. (2013) studied the symbiotic performance of two *Mesorhizobium ciceri* strains (salt sensitive and salt tolerant), transformed with an exogenous 1-aminocyclopropane-1-carboxylate deaminase gene (*acdS*), in chickpea plants under salinity stress. They demonstrated that by expressing an exogenous *acdS* gene, a salt sensitive *Mesorhizobium* strain was able to induce nodules in chickpea plants to the same extent as a salt-tolerant strain. Furthermore, the use of *acdS*-expressing rhizobia protected chickpea plants from salinity stress-induced symptoms. Kumari and Khanna (2015) showed that *Mesorhizobium ciceris* isolates producing ACC-deaminase enhanced chickpea growth especially under salt stress. Overall, as described by Singh et al. (2015), the ACC deaminase is a natural weapon produced by diverse bacteria against “stress ethylene”. The role of ACC deaminase-producing bacteria in protecting plants from the harmful effects of salt as well as improving plant growth is widely reported suggesting the importance of their application in the future as bio-fertilizers.

The increased level of ethylene produced by the stressed legumes inhibits the IAA (indole-3-acetic acid, auxin) signal transduction thereby limiting IAA synthesis and transport

(Sanyal and Bangerth 1998), which consequently inhibit root elongation. It has been demonstrated that plant mutants with defects in auxin transport were more sensitive to salt stress (Korver et al. 2018). Furthermore, salt stress affects auxin transport by altering the expression of *PIN* genes involved in auxin polar transport leading to a reduction in root meristem size (Liu et al. 2015a, b). In soybean, the *GmPIN* (a legume-specific *PIN* gene) is down-regulated by salt (Wang et al. 2015b), suggesting that IAA transport between plant cells affects plant response to saline conditions. Many rhizobacteria can synthesize IAA. *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Microbacterium* are among the most active IAA producers (Tsavkelova 2011). The synthesized and secreted IAA is taken up by plant cells, which can stimulate plant cell proliferation (Glick et al. 2007). It can also promote the growth of primary and lateral roots (Ivanchenko et al. 2010) and alleviate some of the adverse effects of salt stress. The exogenous IAA enhanced the yield of faba beans under high salinity conditions (Abdel Latef et al. 2021). The IAA interferes with lipid peroxidation and/or dissociates malondialdehyde accumulated by salt-induced oxidative damage by improving antioxidant enzymes, including Superoxide dismutase (SOD), Catalase (CAT), Glutathion Peroxidase (GPX), and Ascorbate Peroxidase (APX) (Abdel Latef et al. 2021). It has been reported that increased IAA can stimulate

ACC synthase (VR-ACS1) transcription and reduce the gene expression level of ACC oxidase (*VR-ACO1*) transcripts in mung bean (Kim et al. 2001), suggesting that IAA participate in the regulation of ethylene production. The bacteria that produce both IAA and ACC deaminase possess a significant advantage over those producing only IAA, since they can decrease ACC due to increased IAA action. IAA enhances the transcription of ACC synthase. A large amount of ACC is liberated by root, taken up by bacterial cells and finally cleaved by ACC deaminase (Gamalero and Glick 2015). As a result, IAA improves plant growth and ACC deaminase decreases ethylene production.

ABA is a key phytohormone involved in signaling pathways against abiotic stress. When plants face salinity stress, ABA regulates stress-response genes, such as Response-to-Dehydration 29A (*RD29A*), which originates from enhancement of *DREB2* activity, the ABA-responsive gene (*RAB18*) and delta 1-pyrroline-5-carboxylate synthetase (*P5CS*) (Kaushal and Wani 2016). The abscisic acid-response element-binding proteins (AREBs) and bZIP transcriptional factors, are known to mediate gene activation pathway related to abiotic stress tolerance by recognizing ABA in plants (Uno et al. 2000). Some rhizobacteria such as *Azospirillum* sp. and *Pseudomonas* sp. were reported to increase further ABA accumulation in leaves, thus conferring better tolerance to plants (Naz and Bano 2015). Those bacteria upregulate 9-cisepoxycarotenoid dioxygenase 1 (*NCED1*) and abscisic acid-response element-binding proteins 1 (*AREB1*) genes (Yoo et al. 2019). The enzyme 9-cisepoxycarotenoid dioxygenase (*NCED*) is key in the biosynthesis of ABA in plants (Liu et al. 2016); highly induced by abiotic stresses leading to ABA accumulation. The overexpression of the *NCED* gene caused over-production of ABA, and enhanced abiotic stress tolerance (Thompson et al. 2000). Furthermore, the ABA induce antioxidant enzymes production in root nodules by stimulating the expression of antioxidant genes encoding Cu/Zn-SOD, Mn/Fe-SOD and CAT, and increasing SOD, CAT, GPX and APX activities in plant tissues and root nodules (Palma et al. 2014). This induction is a result of ABA accumulation in plants tissues subjected to salinity stress. Asensio et al. (2012) demonstrated that ABA stimulates Fe-SOD synthesis in all plant tissues of soybean under stress, underscoring the important role of ABA as a signal molecule in the activation of the nodular antioxidant metabolism.

Antioxidants in plants and nodules include a host of enzymes and metabolites that function to eliminate ROS (synthesized by stressed host legumes). Higher tolerance is associated with reduced lipid peroxidation, higher activities of SOD, CAT, peroxidase (POD), and APX as well as higher concentrations of reduced glutathione (GSH) and soluble sugar in nodulated roots under salt stress (Wang et al. 2016a, b; Irshad et al. 2021). Superoxide dismutase (SOD) acts as

a first line of defense against superoxide radical (O_2^-). SOD catalyzes the conversion or dismutation of toxic O_2 radicals to H_2O_2 and molecular oxygen (O_2). The H_2O_2 is subsequently detoxified to water (H_2O) by CAT or GPX (Wang et al. 2016a, b). Four groups of SOD exist including copper-zinc superoxide dismutase (Cu/Zn-SOD), manganese superoxide dismutase (Mn-SOD) and iron superoxide dismutase (FeSOD) (Miao and St. Clair 2009). Cu/Zn-SOD are located within the cytosol and plastids, whereas Fe/Mn-SODs are usually located within organelles, such as mitochondria. So far, cambialistic SOD (Cam-SOD) has been discovered (Asensio et al. 2012). Cam-SOD may have either Fe or Mn as a ligand and is of bacterial origin. They are the most active SOD in response to oxidative stress and have principally *Rhizobium* endosymbiont origin (Asensio et al. 2012). Catalase (CAT) is a common antioxidant enzyme present in almost all living tissues that utilize oxygen. The enzyme uses either iron or manganese as a cofactor and catalyzes the reduction of hydrogen peroxide (H_2O_2) to water and molecular oxygen, consequently completing the detoxification process initiated by SOD. CAT is highly efficient; it can break down millions of hydrogen peroxide molecules in one second (Ighodaro and Akinloye 2018). Glutathione Peroxidase (GPX) is an important intracellular enzyme that breakdown hydrogen peroxide (H_2O_2) to water; and lipid peroxide to their corresponding alcohols mainly in the mitochondria and sometimes in the cytosol (Ighodaro and Akinloye 2018). Several studies demonstrated that the presence of *Rhizobium* sp. under salinity stress decreased APX and GPX activity in the plant, while activity of CAT increased (Matamoros et al. 2003; Rabiei et al. 2020). In nodules, CAT was found to be the main enzyme involved in H_2O_2 scavenging in faba bean (Fatnassi et al. 2015). The antioxidant machinery in legume plants helps them to overcome the adverse effect of salinity by protecting them from oxidative stress. In addition, the rhizobia play an important role in increasing the activity of those antioxidants, which confer tolerance to salt and promote plant growth under stressful conditions.

Bacterial exopolysaccharides (EPS) are necessary for a functional *Rhizobium*-legume symbiosis in both favorable and salt stress conditions. It helps plants to mitigate salinity stress by fixing sodium ions in the soil, reducing their absorption by the plant and preventing these ions from reaching the stem, thereby increasing nutrient uptake by roots (Bhagat et al. 2021). EPS are high-molecular weight polymers attached to the outer surface of bacteria. Those acidic polysaccharides are responsible for bacterial cells attachment to surfaces including plant roots and soil particles and enhance the soil fertility and nutrient transport to roots (Forni et al. 2017). Another mechanism used by EPS to impart salt-tolerance to plants is their ability to establish a biofilm (Benidire et al. 2020). Increased concentration of salt induces an increase in EPS production, which triggers

biofilm formation and sodium chelation, thus reducing the adverse effect of salt stress on plant growth (Bhagat et al. 2021). EPS production is co-regulated with Nod factors, but the type of co-regulation varies depending on the rhizobial strain (Acosta-Jurado et al. 2021). *RosR*, a gene encoding a positive transcriptional regulator of EPS synthesis in *R. leguminosarum* (Janczarek and Skorupska 2007). The *RosR* mutants produced three times less exopolysaccharide than wild type, decreased attachment and colonization of root hairs and were defective in biofilm formation (Janczarek et al. 2010). In addition, *prsD* and *prsE* genes are responsible for secretion of the exopolysaccharide (EPS)-glycanases PlyA and PlyB and are involved in biofilm formation by *Rhizobium leguminosarum* (Russo et al. 2006). The mutant disrupted in *prsD* and *prsE* genes engendered an immature biofilm formation with an atypical structure. A mutation or deletion in the *psaA* genes, which encode the first IP-gluco-syl transferase abolished the ability of *R. leguminosarum* to develop a biofilm (Russo et al. 2006). A number of studies have shown that the expression of succinoglycan (EPS I) and galactoglucan (EPS II) of *Rhizobium meliloti*, is regulated at the transcriptional level by ion concentrations. *ExpR* regulates genes that play a role in salt tolerance (Lloret et al. 1998; Miller-Williams et al. 2006). The role executed by

EPS argue the potential of EPS-producing bacteria and recommends their use for salinity-stress management strategies.

Salt stress alleviation strategies in legume plants

Numerous strategies were applied to improve legume growth, particularly under salinity stress and to mitigate the adverse effect of salt at different stages of plant development (Fig. 4). Biological, chemical, and physical treatments were successfully applied to seeds, seedlings, or plants to enhance tolerance to salt stress as well as the identification of salt-adapted cultivars in saline areas, breeding for plant salt tolerance and introducing new genes for salt tolerance into legume plants (Table 2).

Plant growth promoting bacteria

Soil is an abundant source for microorganisms, particularly in the rhizosphere, the layer of soil influenced by plant root. Among these different microorganisms, bacteria are the most common (Glick 2012). In unstressed soils, up to 10^8 or 10^9 microbial cells per gram of soil can exist. However, the

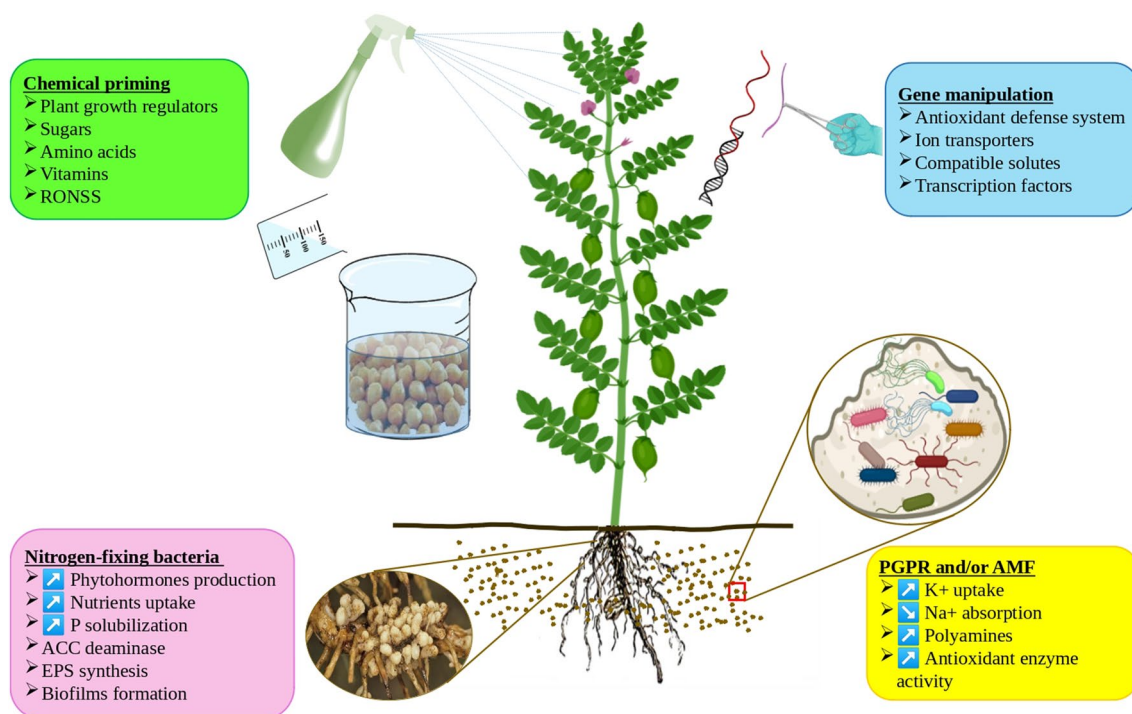


Fig. 4 Schematic representation of the main strategies for salt stress alleviation in legumes. These approaches include chemical priming of seeds and plants using natural and/or synthetic substances, the use of nitrogen-fixing bacteria, PGPR alone or in association with AMF or gene manipulation (Knock-out, knock-down and overexpression strat-

egies). At the end, these alleviation approaches increase plant survival and productivity under salt stress conditions by: (i) improving nutrient uptake, (ii) stimulating the antioxidant defense machinery, (iii) enhancing the production of compatible solutes and (iv) activating plant defense mechanisms

Table 2 Overview of the main salt alleviation strategies applied to legume plants that have been reported in previous studies

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References
Plant growth promoting bacteria and rhizobia	<i>Arachis hypogaea</i> L.	Inoculation with <i>Brachylobacterium saurashtrense</i> , <i>haererothalobacter</i> , and <i>Brevibacterium casei</i>	Increased plant growth and biomass under saline conditions	Shukla et al. (2012)
	<i>Cajanus cajan</i>	Inoculation with <i>Bradyrhizobium</i> , and <i>Burkholderia cepacia</i>	Pigeon pea co-inoculation with <i>Bradyrhizobium</i> and <i>Burkholderia cepacia</i> strains reduced the accumulation of Na ⁺ ions This increased growth when exposed to salt stress	Bano et al. (2015)
	<i>Cicer arietinum</i>	Triple inoculation with <i>Rhizobium</i> , mycorrhizal fungi, and <i>Stenotrophomonas maltophilia</i>	Improved nutritional status of chickpea plants occurring as a result of the enhancement of K, P, carbohydrate, and protein contents Increased leghemoglobin content and nitrogenase activity under salt stress conditions	Abd-Alla et al. (2019)
	<i>Glycine max</i>	Inoculation with <i>Sinorhizobium meliloti</i>	Chickpea plants' nutritional status has improved as a result of higher K, P, carbohydrate, and protein contents Leghemoglobin concentration and nitrogenase activity were elevated when exposed to salt stress Increased growth attributes and chlorophyll content in salt-stressed soybean plants	Qu et al. (2016) Khan et al. (2019)
		Inoculation with <i>Arthrobacter woluwensis</i> , <i>Microbacterium oxydans</i> , <i>Arthrobacter aureescens</i> , <i>Bacillus megaterium</i> , and <i>Bacillus aryabhatai</i>	increased ability to withstand salt stress by altering the architecture of the root system, which is still advantageous for nutrient uptake and nodule production	Egamberdieva et al. (2017)
		Co-inoculation with <i>Pseudomonas putida</i> and <i>Bradyrhizobium japonicum</i>	The shoot and root growth, shoot biomass, seed weight, and grain yield all increased	Ilangumaran et al. (2021)
		Co-inoculation of <i>Rhizobium</i> sp. and <i>Hydrog-enophaga</i> sp. with <i>Bradyrhizobium</i>	Improved salt-tolerance of soybean plants through the stimulation of plant growth attributes and nodulation	Kang et al. (2014a, b)
		Inoculation with <i>Pseudomonas putida</i>	Improved characteristics of seed germination and plant growth, and promoted isoflavone biosynthesis	Khan et al. (2011)
	<i>Lens culinaris</i>	Inoculation with <i>Penicillium funiculosum</i>	Growth attributes, namely shoot and root fresh weights and lengths improved with the bacterial inoculation Even under salt-stress situations, higher chlorophyll concentration	Muscolo et al. (2019)
		Inoculation with <i>Pseudomonas putida</i> , <i>Pseudomonas fluorescens</i> , and <i>Serratia ficaria</i>		

Table 2 (continued)

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References
	<i>Medicago sativa</i>	Inoculation with <i>Klebsiella</i> sp., <i>Kosakonia cowanii</i> , and <i>Sinorhizobium meliloti</i>	Increased growth indicators for alfalfa Reduced Na ⁺ accumulation and increased K ⁺ absorption, resulting in a decrease in K ⁺ /Na ⁺ ratio Higher proline content and a strong CAT and SOD antioxidant activities	Noori et al. (2018)
	<i>Phaseolus mungo</i>	Co-inoculation of <i>Rhizobium meliloti</i> and <i>Pseudomonas fluorescens</i>	Increased N and P amounts and decreased Na ⁺ contents, resulting in a better salt tolerance	Younesi et al. (2013)
	<i>Pisum sativum</i>	15 rhizobia strains tested for the inoculation	Improved chlorophyll content, plant growth and biomass	Yasin et al. (2018)
	<i>Pisum sativum</i>	Inoculation with <i>Arthrobacter protophormiae</i>	Increased plant tolerance to salinity by improving colonization of a diverse bacterial population and increasing ACC deaminase activity	Barnawal et al. (2014)
	<i>Vicia faba</i>	Inoculation with <i>Rhizobium leguminosarum</i>	Reduced Na ⁺ , Ca ²⁺ , and K ⁺ absorption by faba bean plants Increased plant biomass, nitrogen content and nodule number	Benidire et al. (2017)
		<i>Pseudomonas putida</i> co-inoculation with <i>Pseudomonas fluorescens</i> and <i>Bacillus subtilis</i>	Enhanced plant growth attributes, mainly plant height, fresh shoot weight, and leaf area	Metwali et al. (2015)
		Inoculation with <i>Azotobacter chroococcum</i>	Enhanced soil fertility and improved plant growth under salt stress conditions due to biofilm formation and EPS production by bacterial strain	Mohammed (2018)
		Combined action of <i>Azotobacter chroococcum</i> and melatonin	Increased faba bean growth attributes and yield components under salt stress Enhanced N, P, and K amounts, proline content, and K ⁺ /Na ⁺ ratio	Abd El-Ghany and Attia (2020)
	<i>Vigna radiata</i> L.	Inoculation with <i>Pseudomonas syringae</i> , <i>Pseudomonas fluorescens</i> , and <i>Rhizobium phaseoli</i>	Reduced ethylene synthesis and promoted nodulation under salt stress conditions	Ahmad et al. (2011)
		Inoculation with <i>Pantoea</i> sp. and <i>Enterococcus</i>	Increased tolerance to salt stress as a result of the bacteria's powerful ACC deaminase and plant growth-promoting abilities	Panwar et al. (2016)
	<i>Vigna unguiculata</i>	Inoculation with Rhizobia strains	Increased cowpea growth attributes and yield	Nyaga and Njeru (2020)

Table 2 (continued)

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References
Arbuscular mycorrhizal fungi	<i>Cajanus cajan</i> L.	Inoculation with <i>Rhizophagus irregularis</i> and <i>Funneliformis mosseae</i>	Increased plant biomass, yield, and nutrient absorption under salt stress conditions Enhanced membrane stability achieved by maintaining proper K^+/Na^+ and Ca^{2+}/Na^+ ratios Improved nodulation and leghemoglobin content along with the SOD, APOX, GR, POX, and CAT activities Reduced membrane permeability and lipid peroxidation Enhanced plant tolerance to salt stress	Garg and Pandey (2015) Garg and Manchanda (2008)
		Inoculation with <i>Glomus mosseae</i>	Improved plant tolerance to salt stress	
		Inoculation with AMF strains	Improvements in nodule dry mass, nitrogenase activity, and phosphorus amount under salt stress Enhanced antioxidant enzyme activities, thus alleviating the toxic effects of salt stress	Manchanda and Garg (2011)
	<i>Cicer arietinum</i> L.	Inoculation with <i>Glomus mosseae</i> and <i>Acaulospora laevis</i>	Enhanced host plant mineral concentration and increased plant growth and yield under salt stress conditions	Kadian et al. (2013)
	<i>Lens culinaris</i>	Inoculation with AMF isolates	Enhanced seed germination percentage, seed and stover yield under saline conditions	Rahman et al. (2017)
	<i>Medicago sativa</i>	Inoculation with <i>Glomus mosseae</i>	Increased nodule number, dry weights, and nitrogenase activity, resulting in better plant growth and nitrogen fixation under salt stress	Moradi (2016)
		Inoculation with <i>Glomus mosseae</i>	Increased proline and soluble protein concentrations, plant height, biomass, and plant survival rate Increased the amount of osmotic control compounds, which helped plants grow better in saline-alkaline soils	Zhao and Bao (2015)
	<i>Vicia faba</i>	Inoculation with <i>Funneliformis mosseae</i> , <i>Rhizophagus intraradices</i> , and <i>Claroideoglossum etunicatum</i>	Increased nodule activities and pigment contents, and improved K and Ca accumulation under salt stress Improved growth and plant yield under salt stress conditions	Abeer et al. (2014)
	<i>Vigna unguiculata</i>	Inoculation with AMF strains	Salt stress led to a rise in the activity of several enzymes, including catalase, superoxide dismutase, ascorbate peroxidase, peroxidase, and glutathione reductase A higher level of salt stress resistance in plants as a result of enhanced nitrogen uptake	Abeer et al. (2015)

Table 2 (continued)

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References	
Seed and plant priming	<i>Glycine max</i> L.	Seed priming with Potassium nitrate	Enhanced emergence and germination percentage Improved plant dry weight, radical and plumule length	Ahmadvand et al. (2012)	
	<i>Pisum sativum</i>	Seed priming with Polyethylene glycol	Increased germination percentage	Khalil et al. (2001)	
		Seed priming with Salicylic acid	Improved photosynthetic efficiency and stronger plant antioxidant defense system result in a better tolerance to salt stress	Ahmad et al. (2017)	
	<i>Vicia faba</i> L.	Seed priming with Salicylic acid	Reduced the inhibitory effects of salt stress on seed germination Increased growth attributes, total chlorophyll content, soluble carbohydrate content, and antioxidant activities	Azooz (2009)	
		Seed priming with Salicylic acid	Prevented the negative effects of salt stress Enhanced IAA and IBA amounts and decreased ABA levels	Ahmad et al. (2018)	
Breeding		Seed priming with Salicylic acid	Decreased the salt stress-induced growth interruption	Anaya et al. (2018)	
		Seed priming with Salicylic acid and hydrogen peroxide	Improved seeds' fresh, dry weights and germination An increase in sugar accumulation, alpha amylase, and antioxidant activities, which promotes primary root elongation and seed germination	Bouallègue et al. (2017)	
	<i>Vigna radiata</i> L.	Seed priming with sodium chloride	Increased chlorophyll content and osmolytes buildup A strengthened antioxidant defense mechanism, which reduces the damaging effects of salinity on mung bean plants	Saha et al. (2010)	
	<i>Cicer arietinum</i> L.	Image based phenotyping	The primary factor of chickpea salt tolerance has been identified: seed number	Atieno et al. (2017)	
		Comparative transcriptome analysis (HiSeq-2500)	Up-regulation of transcripts encoding potassium transporter family HAK/KUP proteins, MIP/aquaporin protein family, NADH dehydrogenase, pectinesterase, and PP2C family proteins under salt stress	Kumar et al. (2021)	
	<i>Lens culinaris</i>	GWAS	Potassium transporters have been identified as the most likely indicator of salt stress tolerance	Dissanayake et al. (2021)	
	<i>Medicago sativa</i>	Comparative transcriptome analysis	Differentially expressed genes by salt stress have been identified. The DEG are associated with calcium, redox, and hormone signaling	Kaundal et al. (2021)	

Table 2 (continued)

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References
	<i>Medicago truncatula</i>	Comparative transcriptome analysis	Identification of specific gene clusters associated with the auxin pathway, modified histone variant isoforms, and selectively controlled by salt in root apices	Zahaf et al. (2012)
	<i>Phaseolus vulgaris</i>	Comparative transcriptome analysis	Identification 441 transcription factors and differentially expressed genes in response to salt stress	Hiz et al. (2014)
	<i>Pisum sativum</i> L.	QTL mapping	Identification salt tolerance QTLs on linkage groups Ps III and VII with flanking SNP markers?	Leonforte et al. (2013)
	<i>Vicia faba</i> L.	Conventional breeding	Given that salt stress had no impact on plant growth or nitrogen fixation, the VF112 line was identified as salt tolerant	del Pilar et al. (1995)
		Conventional breeding	Identification of the salt tolerant genotypes: Fiesta VF, Acc 1512/2 and Acc 1487/7/ based on yield-related characteristics	Tavakkoli et al. (2012)
		Conventional breeding	Identification of "water-stress-day index" as the best predictor for yield	Katerji et al. (2003)
		Conventional breeding	Identification of salt-tolerant cultivar "Giza 8-43" with greater osmotic adjustment ability and higher proline and nutrient contents	Orabi and Abdelhamid (2016)
	<i>Vigna radiata</i> L.	SNP-based genome wide association	Identification of leaf osmotic potential and photosynthesis rate as the main determinants of salt tolerance	Tavakkoli et al. (2010)
	<i>Arachis hypogaea</i>	Heterologous expression of <i>Arabidopsis DREB1A</i> gene	Identification of salt tolerance-associated SNPs on chromosomes 7 and 9	Breria et al. (2020)
Gene manipulation	<i>Glycine max</i> L.	Introduction of <i>Arabidopsis vacuolar Na⁺/H⁺ antiporter gene (AtNHX1)</i>	Enhanced plant growth attributes include proline, chlorophyll contents, electrolyte leakage, and osmotic potential	Sarkar et al. (2014)
		Overexpression of <i>GB1</i> gene	Improved plant growth under salt stress circumstances by reducing the harmful effects of salt stress	Li et al. (2010)
		Overexpression of <i>GmNAC085</i> gene	Improved Na ⁺ homeostasis	Castiglioni et al. (2018)
		Overexpression of soybean <i>GmMYB84</i> gene	Increased glycine betaine levels in salt-stressed soybean plants	Hoang et al. (2021)
			Increased antioxidant enzyme activities, proline contents, and dehydrin accumulation in salt stress conditions	
			Increased seed germination, primary root elongation, proline accumulation, membrane integrity, antioxidant enzyme activity, and K ⁺ levels	Zhang et al. (2020)

Table 2 (continued)

Alleviation strategy	Legume plants	Applied treatment/approach	Notable effects	References
		Overexpression of soybean <i>GmDREB6</i> gene	Improved proline accumulation and salt tolerance in genetically modified soybean plants	Nguyen et al. (2019b)
		Knock-out of the ABA-induced transcriptional repressors; AITRs genes	Improved plant growth under salt stress in AITR mutants generated using CRISPR-Cas9 technology	Wang et al. (2021)
		CRISPR-Cas9 silencing of <i>GmNAC06</i> gene	Enhanced proline and glycine betaine accumulation along with better regulation of Na^+/K^+ ratio	Li et al. (2021)
		Overexpression of <i>GmNHX5</i> gene using CRISPR/Cas9 technology	Enhanced K^+/Na^+ ratio under salt stress conditions	Sun et al. (2021)
			Up-regulation of <i>GmSOS1</i> and <i>GmSKOR</i> genes, encoding the plasma membrane Na^+/H^+ antiporter and sodium/hydrogen exchanger, respectively	
	<i>Medicago sativa</i>	Overexpression of a <i>plastid glycogen synthase kinase 3</i> encoding gene (<i>MsK3</i>)	Enhanced starch and glucose levels result in better tolerance to salt stress	Andersen et al. (2007)
		Overexpression of <i>Alfin1</i> gene	Enhanced endogenous <i>MsPRP2</i> levels result in better tolerance to salt stress	Winicov and Bastola (1999)
	<i>Medicago truncatula</i>	Introduction of cyanobacterial flavodoxin	Improved the symbiotic performance under salt stress by inducing significant changes in enzymatic activities that control nodule redox balance	Coba de la Pena et al. (2010)
	<i>Vicia faba</i>	Heterologous expression of potato <i>PR10a</i>	Increased plant survival under salt stress conditions	Hanafy et al. (2013)
			Improved tolerance to salt resulting from a strong accumulation of proline under stressful conditions	
		Constitutive expression of <i>Arabidopsis</i> vacuolar Na^+/H^+ antiporter gene (<i>AtNHX1</i>)	Improved plant growth under salt stress conditions	Hassanein et al. (2019)
			This alleviated the harmful effects of salinity	
	<i>Vigna radiata</i> L.	Constitutive expression of <i>Arabidopsis</i> vacuolar Na^+/H^+ antiporter gene (<i>AtNHX1</i>)	Improved plant growth attributes under salt stress, namely plant height, foliage, dry mass and seed yield	Kumar et al. (2017)
			Enhanced Na^+ sequestration in roots and prevented Na^+ influx to shoots, resulting in a better intracellular ion homeostasis and osmoregulation	
		Overexpression of <i>Arabidopsis</i> vacuolar Na^+/H^+ antiporter gene (<i>AtNHX1</i>)	Reduced damages imposed by salt stress exposure through maintaining higher K^+/Na^+ in the aerial parts and higher Na^+ levels in roots	Sahoo et al. (2016)
			Reduced lipid peroxidation and ROS accumulation due to the increased antioxidant activity	
	<i>Vigna unguiculata</i> L.	Overexpression of <i>Vu NHX1</i> gene in <i>Arabidopsis</i>	Improved plant tolerance to salinity, enhanced proline and chlorophyll contents	Mishra et al. (2015)
			This maintained the K^+/Na^+ ratio at a high level, resulting in better ion homeostasis	

number of bacteria may be as low as 10^4 cells per gram of soil in stressed soils (Timmusk et al. 2011). The term plant growth-promoting bacteria (PGPB) is employed to encompass all these bacteria that enhance plant growth (Kang et al. 2014a). The PGPB occupy mainly roots surrounding soil (Orozco-Mosqueda et al. 2020). The most widely exploited and studied group of PGPB are plant growth-promoting rhizobacteria (PGPR) that have the capacity to colonize the root surfaces and closely adhere to the rhizosphere (Klopper et al. 1999).

The PGPB is an alternative strategy to alleviate salt stress and boost the growth of salt-stressed crops. PGPB can be used as a cost effective way to increase salinity tolerance and promote plant growth (Numan et al. 2018). The PGPB can stimulate plant growth by secreting plant growth substances in the absence of biotic or abiotic stress, facilitating resource acquisition or modulating plant hormone levels. Some PGPB also have specialized mechanisms that play a key role in salt stress tolerance and plant growth promotion. These bacteria trigger plants to produce different plant growth hormones like auxin, cytokinin and gibberellin as well as volatile organic compounds. The PGPB fix nitrogen, solubilize organic and inorganic phosphate and also produce siderophore, which improve plant Fe nutrition (Numan et al. 2018). Besides, PGPB can operate as biocontrol, a widely recognized mechanisms based on a competition for an ecological niche or a substrate, the production of inhibitory allelochemicals (iron-chelating, siderophores, antibiotics, biocidal volatiles, lytic enzymes, and detoxification enzymes), and the induction of systemic resistance (ISR) in hostplants to a broad spectrum of pathogens and/or abiotic stresses (Compant et al. 2005).

The ameliorative effects of PGPR on legume growth under saline conditions have been proven in multiple legume species including faba bean (Benidire et al. 2017), soybean (Qu et al. 2016), alfalfa (Noori et al. 2018), pigeon pea (Bano et al. 2020), cowpea (Nyaga and Njeru 2020), lentil (Muscolo et al. 2019) and chickpea (Abd-Alla et al. 2019) (Table 2). PGPR display their beneficial features to overcome the toxic effects of high NaCl on morphological, physiological, and biochemical processes in plants, resulting in a significant rescue of yield loss (Ha-Tran et al. 2021). The inoculation of *Arthrobacter woluwensis*, *Microbacterium oxydans*, *Arthrobacter aureus*, *Bacillus megaterium*, and *Bacillus aryabhatai* increased plant growth attributes and chlorophyll content in soybean plants under 200 mM NaCl stress (Khan et al. 2019). The use of salt-tolerant species of *Pseudomonas* has been reported to improve legume health. For instance, *Pseudomonas putida* co-inoculated with *Pseudomonas fluorescens* and *Bacillus subtilis* on the growth of six faba bean cultivars under salinity stress enhanced plant height (10.66%), shoot fresh weight (9.52%), and plant leaf area (61.86%) (Metwali et al. 2015).

In addition, Egamberdieva et al. (2017) indicated that the inoculation of salt-tolerant *P. putida* with *Bradyrhizobium japonicum* synergistically improved soybean salt tolerance through the modification of the root system architecture, which can facilitate nitrogen and phosphorus acquisition, and nodule formation.

PGPB can stimulate plant growth during salt stress through several mechanisms including N_2 fixation, phytohormone production, amelioration of nutrient uptake, aminocyclopropane-1-carboxylic acid deaminase production, phosphorus solubilization, exopolysaccharide (EPS) synthesis, iron acquisition, and biofilm formation (Mokrani et al. 2020). Mohamed et al. (2018) studied the production of biofilm and EPS by plant growth-promoting rhizobacteria (PGPR) under different salt concentrations. They demonstrated that biofilm formation and EPS-production by *Azotobacter chroococcum* significantly contribute to soil fertility and improve faba bean growth. Furthermore, the combination of EPS-producing bacteria (*Az. chroococcum*) and melatonin significantly increased the growth parameters and yield components in faba bean grown in the presence of salt stress (Abd El-Ghany and Attia 2020). Both bacteria inoculation and melatonin application enhanced N, P, and K concentrations; proline content; relative water content (RWC); and the K^+/Na^+ ratio. In addition, Na^+ and Cl^- concentrations decreased significantly in salt-stressed faba beans (Abd El-Ghany and Attia 2020). Furthermore, PGPR can stop the expression of plant genes that increase plant sensitivity under salinity stress. For example, Pi et al. (2019) demonstrated that PGPR inhibited the phosphorylation of the gene encoding a cytochrome P450 monooxygenase, which contributes to the accumulation of monohydroxy B-ring flavonoids that negatively regulate soybean tolerance to salinity. The application of PGPR inoculants is among the best way to overcome the adverse effect of salinity and increase tolerance to this stress. Almost success of PGPR application was proven in the laboratories and green house. Nevertheless, the challenge now is its large-scale use in the field, its adoption as a future biofertilizer as well as its sustainability in agriculture. Therefore, the research should focus more on the widespread application of PGPR in the field.

Rhizobia–Legume symbiosis

Symbiosis is one of the alternatives to mitigate the adverse effect of salinity and to discover new mechanisms involved in stress tolerance (Dodd and Pérez-Alfocea 2012). Several studies have demonstrated that plant–microbe interactions prompt abiotic stress tolerance along with growth and biomass (Kumar and Verma 2018). The Legume–*Rhizobium* symbiosis is a highly integrated system that leads to biological nitrogen fixation (Cordovilla et al. 1995). About 40 rhizobia species within seven genera known to nodulate and

fix nitrogen with legumes have been identified and includes *Rhizobium*, *Allorhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, and *Methylobacterium* (Lemaire et al. 2015). The legume–rhizobia association is highly specific. For instance, *Rhizobium* strains are largely associated with pea (*Pisum sativum*), lentil (*L. culinaris*), faba bean (*V. faba*) and common bean (*P. vulgaris*), while *Bradyrhizobium* strains often nodulate soybean (*G. max*), cowpea (*Vigna unguiculata*), lupine (*Lupinus albus*) and peanut (*A. hypogaea*) plants. Finally, chickpea (*C. arietinum*) is mostly nodulated by different species belonging to the *Mesorhizobium* genus (Silva et al. 2017; Koskey et al. 2018). In faba bean, the identification of rhizobia from nodules indicates that the most common species are *Rhizobium leguminosarum* bv. *Viciae* (Mutch and Young 2004), *Rhizobium fabae* (Tian et al. 2008), *Rhizobium laguerreae* (Saïdi et al. 2014) and *Rhizobium anhuiense* (Zhang et al. 2015).

It is known that rhizobia strains vary in their salt tolerance. For example, *B. japonicum*, *Rhizobium etli*, and *R. leguminosarum* are salt sensitive with their growth inhibited completely at 100 mM NaCl (Boncompagni et al. 1999). Nevertheless, some rhizobacteria can be halotolerant to salt stress. For instance, *Rhizobium* spp. isolated from nodules of *Leucaena*, *Acacia*, *Prosopis* and *Hedysarum* plants can tolerate up to 500 mM NaCl (Zhang et al. 1991). Rhizobacteria isolated from saline habitats can be more efficient at enhancing plant tolerance to salt than those isolated from non-saline habitats (Etesami and Beattie 2018). In saline soils in Morocco, Benidire et al. (2017) isolated two indigenous strains of *R. leguminosarum* (RhOF34 and RhOF125). The isolated strains improved nodulation, increased plant biomass and N content in faba bean and induced plant protection against salinity. The co-inoculation of rhizobia with other rhizobacteria improves also the growth and development of the host-legume. Ilangumaran et al. (2021) co-inoculated *Rhizobium* sp. SL42 and *Hydrogenophaga* sp. SL48 with *Bradyrhizobium* which resulted in higher growth soybean plants than the *Bradyrhizobium* control. *Rhizobium* and *Pseudomonas* co-inoculation moderated the negative effects of salinity in alfalfa (*M. sativa*) and significantly increased P and N contents while Na⁺ accumulation decreased (Younesi et al. 2013). Several studies reported that the inoculation of different genera and species of rhizobia in several grain legumes affected host plant metabolism and increased antioxidant and other compatible solutes accumulation, which can ultimately lead to better tolerance under salinity stress. Qu et al. (2016) found that *Sinorhizobium meliloti*-1021 played significant roles in regulating the transcription of several key enzymes related to flavonoids metabolism, which can lead to a significant increase in soybean's tolerance to salt. In addition, Irshad et al. (2021) explained the improved salt tolerance in inoculated *M. sativa* plants with *R. meliloti* with higher activities of enzymatic and nonenzymatic

antioxidants and higher compatible solutes synthesis (proline, free amino acids, glycine betaine, soluble sugars, and proteins) when compared with non-inoculated plants.

Arbuscular mycorrhizal fungi

Many reports solicited other microorganisms such as *Mycorrhiza* to be used as inoculants under unfavorable and stressful environmental conditions. The symbiotic relationship between mycorrhiza and roots is abundant in nature. The AMF is the most common type of this symbiosis, which has a great ecological and economic importance. The AMF symbiosis is a key component in helping plants to cope with salt stress and in increasing salinity tolerance, as demonstrated in a number of host plant and fungal species (Yang et al. 2014; Evelin et al. 2019; Wang et al. 2020). In faba bean, AMF acts as a stimulator of plant growth under salt stress. It helps plant to overcome the negative effects of NaCl by increasing nodules activities and pigments contents, which improves plant growth and yield. Furthermore, AMF also restores K and Ca contents and maintains their ratios under salt stress (Hashem et al. 2014). When plants form a symbiotic relationship with fungi, changes occur in their morphology, nutrition, and physiology, increasing their resistance to abiotic stress. AMF supply mineral nutrients to plants, especially phosphorus, which is precipitated by ions such as Ca²⁺, Mg²⁺, and Zn²⁺ (Al-Karaki et al. 2001). AMF can also improve photosynthesis in plants exposed to salt stress (Chen et al. 2017). In addition, mycorrhizal symbiosis facilitates K⁺ uptake and intercept Na⁺ absorption and translocation to the shoots (Chang et al. 2018; Liu et al. 2019). Application of AMF also increases polyamines: nitrogenous compounds that have been proven effective in alleviating NaCl stress (Hashem et al. 2014). Antioxidant enzyme activities like SOD, CAT, POD and APX are the main defense for legumes against NaCl stress and mycorrhiza treated legumes showed greater increase in antioxidant activities (Hashem et al. 2014). In addition, plants' inoculation with AMF showed enhancement in nodule activity and pigment content under salt stress conditions (Hashem et al. 2014).

The positive impact on plant growth and stimulation of stress tolerance by synergistic interactions of PGPR and AMF under hostile environments was also mentioned. An improvement in faba bean-rhizobia symbiotic performance by AMF has been reported (Yinsuo et al. 2004), as well as other legume species such as lentil (Xavier and Germida 2002), common bean (Tajini et al. 2012), alfalfa (Ashrafi et al. 2014) and chickpea (Abd-Alla et al. 2019). The synergistic interactions among the components of the tripartite symbiotic association (*Rhizobium*–AMF–faba bean) increased the photosynthetic rate and plant productivity. Accordingly, Dubova et al. (2015) have underlined that

rhizobia-mycorrhizae inoculation showed better improvement of faba bean growth in saline soil compared to simple inoculation with mycorrhizae (Dubova et al. 2015). Furthermore, Rabie and Almadini (2005) examined tripartite interactions among a bacterium (*Azospirillum brasilense*), an arbuscular mycorrhizal fungi (*Glomus clarum*), and faba bean under increased NaCl levels. Significant positive effects of inoculation were observed in plants with respect to salinity tolerance, mycorrhizal dependence, phosphorus level, phosphatase enzymes, nodule number, nitrogen uptake, protein content and nitrogenase activity. AMF can be an effective bio-fertilizer to improve legume cultivation on saline agricultural lands. Moreover, the consideration of rhizobacteria and AMF interactions could be an exciting alternative to guarantee and increase tolerance to this kind of stress.

Seed and plant priming

Seed and plant priming is a promising, efficient, and low-cost approach to enhance plant tolerance under various abiotic stresses including salinity. Seed priming is defined as a pre-sowing treatment, applied before germination, that allows a partial hydration of seeds and leads to an improvement in seed germination potential, growth and crop's productive capability (Paparella et al. 2015). However, plant priming is a mechanism leading to a physiological state that enables plants to respond more rapidly and/or more robustly after exposure to biotic or abiotic stresses (Aranega-Bou et al. 2014; Costa et al. 2018).

The adverse effect of salinity stress can be alleviated by the use of many chemical priming agents that have a significant impact on plant growth (Ashraf et al. 2018). In faba bean, various priming agents were reported to be efficient in salinity stress alleviation. Some of them are naturally occurring metabolites but also help in stress tolerance when applied exogenously such as sugars, amino acids and their derivatives, plant growth regulators and vitamins (Costa et al. 2018). Under salt stress conditions, they could also play the role of osmoprotectants or antioxidants. Another group of chemical agents called Reactive Oxygen, Nitrogen, and Sulfur Species (RONSS) is also effective in inducing plant tolerance to abiotic stresses. This kind of composite includes NO (nitric oxide), H₂S (hydrogen sulfide) and H₂O₂ (hydrogen peroxide) and plays an important part in plant adaptation to abiotic stress due to their direct impact on gene regulation and signal transduction (Fotopoulos et al. 2015; Ashraf et al. 2018).

It has been reported that seedlings of faba bean primed seeds emerge faster, grow more vigorously and perform better under suboptimal conditions such as salinity stress (Azooz 2009; Anaya et al. 2018). Hormone priming or plant growth regulators have been widely used to increase synchronized seed germination and seedling growth under

salinity stress (Ma et al. 2018). It has also been demonstrated that Salicylic Acid (SA) increases salinity tolerance and seed germination and plant productivity in faba bean (Azooz 2009). Indeed, faba bean seeds primed with salicylic acid stimulated CAT, APX and glutathione reductase (GR) activities under salinity stress (Azooz 2009). Furthermore, the application of SA enhanced the IAA and Indole-3-butyric acid (IBA) and decreased the ABA concentration (Ahmad et al. 2018). The SA supplementation mitigates the negative effects of NaCl toxicity in faba bean seedlings through the modulation of different osmoprotectants, antioxidants and nutrients uptake (Ahmad et al. 2018), and the regulation of the expression of genes involved in germination (Li et al. 2017), resulting in an increase in seedling quality. It is also possible that SA stimulated amylase activity and starch mobilization, thereby, stimulating germination and cell integrity (Bouallègue et al. 2017). Besides, this could be due to the improvement in metabolic activities (including α -amylase activity) caused by SA application resulting in better production of radicle and plumule for seedling development (Anaya et al. 2018).

Melatonin can alleviate the toxicity of oxygen and nitrogen species of faba bean seeds (Moustafa-Farag et al. 2020). Seeds priming with melatonin increased photosynthetic pigments, total carbohydrate, total phenolic content, indole acetic acid, K⁺, Ca²⁺ as well as K⁺/Na⁺ and Ca²⁺/Na⁺ ratios in the leaves under salt stress (Dawood and El-Awadi 2015).

Vitamins priming was also applied to faba bean. Semida et al. (2014) suggested that α -tocopherol could activate antioxidants in plants and decrease oxidative damage, resulting in physiological modifications in plants grown in saline soil. Exogenous application of 200 or 400 mg/L of nicotinamide (vitamin B3) increased nutrient concentrations, sucrose, soluble sugars, free amino acids, oxidative enzymes, photosynthetic pigments, plant growth, seed yield, and seed quality of faba bean salt-stressed plants, while decreasing lipid peroxidation products and the oxidative enzymes (Abdelhamid et al. 2013). Ascorbic acid (AA) priming was highly effective to increase vegetative growth, soluble carbohydrates, proline, free amino acids, K⁺/Na⁺ ratio, and photosynthesis-related pigments in faba bean. AA application improved bean seed germination and seedling growth under salinity stress (Azooz et al. 2013).

Amino acids are fundamental metabolites and plant growth stimulator that significantly mitigate abiotic stress injuries. Amino acid mixture foliar spraying on faba bean plants increased nucleic acid DNA and RNA, total carbohydrates, polysaccharides, photosynthetic pigments, fresh and dry shoot weight, leaf number per plant and shoot length (Sadak et al. 2015). In addition, amino acid application at a rate of 500 or 1000 or 1500 mg/L increased osmotic solutes, phenolic content, IAA, and endogenous polyamine content, while it reduced antioxidant enzymes and lipid peroxidation,

thereby enhancing faba bean tolerance to salt. Exogenous amino acids enhanced free amino acids, proline, and soluble sugars in salt-stressed faba bean (Sadak et al. 2015). Proline provides osmoprotection and facilitates the growth of salt-stressed faba bean plants (Dawood and El-Awadi 2015).

Besides natural priming agent, other agents were also tested. Hellal et al. (2012) showed that Silicon (SiO_2) foliar application alleviates the toxic effects caused by abiotic stresses. The authors observed an increase of the growth parameters of faba bean under salinity. Particularly, the application of 1000 ppm of Silicon significantly improved chlorophyll and carotene content, pod yield and seed number per plant. According to these authors, increased K content and reduced Na in shoots and seeds may be one of the possible mechanisms of the increased salinity tolerance. The improvement of salt tolerance after NSi and Si treatments was due to the improvement of membrane stability, chloroplast formation and sugar accumulation as well as a significant increase in APX, CAT and POD activities in leaves. In addition, the oxidative damage in faba bean, produced by salinity stress, seemed to decrease in accordance with the increase in antioxidant enzymes activity under NSi and Si treatments (Qados 2015).

KNO_3 pre-soaking of faba bean seeds increased the germination percentage and had a significant increase in proline content especially in shoots regardless of the salinity levels used due to a notable decrease in Na^+ and increased K^+ contents (Abdel-Baki et al. 2018). Bouallègue et al. (2017) reported that exogenous application of H_2O_2 to faba bean seeds improved the germination rate and increased primary root elongation under salt stress. This increase was associated with enhanced total amylase activity and total sugar levels and reduced starch content in germinating seeds. For the large-scale use of these approaches in the field, seeds and plant priming can be easily applied and could be a sustainable method to alleviate salinity stress, especially seed priming that only needs seeds' presoaking. A large quantity of seeds can be pre-treated with a little volume of the desired chemical, which will be easy and less expensive in agriculture and can be a promising strategy compared to plant priming that require huge space for foliar application.

Breeding for salt tolerance improvement

Breeding for salt-tolerant genotypes that can grow under high salinity is among the indispensable strategies to alleviate the harmful effects of salt stress. In order to develop legumes with salt stress tolerance, a consistent approach involving the estimation of existing genetic variation, exploiting diverse and novel sources to create new variations, and the use of breeding strategies with several traits instead of a single trait is needed (Duc et al. 2015; Smýkal et al. 2015). For example, Atieno et al. (2017) reported broad genetic

variation for growth rate, days to flower, plant height, leaf senescence, shoot Na^+ and K^+ content, shoot biomass, pod number and seed number under salinity in 245 accessions of chickpea using image-based phenotyping. Similarly, a significant variation was noted among the varieties (Atieno et al. 2017). Furthermore, high coefficients of variation (CV) were registered among four cultivars of faba bean for the different indices of germination under salt stress (El-Bastawisy et al. 2018).

In the last century, plant breeders performed various breeding programs wherein they well implemented the genetic variation of crops at intra-specific, inter-specific, and inter-generic levels to produce salt-tolerant lines and cultivars. As a result, they somewhat succeeded in developing a few salt-tolerant lines or cultivars of several potential crops via traditional breeding (Ashraf and Akram 2009). One example in faba bean is the line "VF112," which has been reported as salt-tolerant because salt stress had no effect on its growth or nitrogen fixation (del Pilar et al. 1995). Other examples of salinity tolerant genotypes such as Fiesta VF, Acc 1487/7 and Acc 1512/2 were also reported (Tavakkoli et al. 2012).

Since the ultimate aim of salt stress tolerance is yield under stress, the traits used for evaluating salt stress tolerance must be correlated with yield and its components (Flowers et al. 2010). Tavakkoli et al. (2012) noted significant variations in salt tolerance degree in eleven faba bean genotypes for yield-related characteristics. Atieno et al. (2017) added that seed number is the major determinant for salinity tolerance measured as yield in chickpea and proposed this trait as a selection trait in breeding salt tolerant chickpea cultivars. Katerji et al. (2003) evaluated nine legume species, including faba bean for salinity tolerance. They found that the best predictor for yield was the 'water-stress-day index', which was the average of the difference in leaf-water potential between the saline and non-saline treatments through the growing season. However, this screening model was clearly not suitable for screening large numbers of genotypes (Stoddard et al. 2006).

Besides, various traits have been used to screen for salt stress tolerance such as seedling emergence, leaf soluble proline, leaf $\text{Ca}^{2+}/\text{Na}^+$, and K^+/Na^+ ratio, stomatal conductance, photosynthetic activity, nodulation and osmotic adjustment. In faba bean, physiological tolerance characterized by the accumulation of high quantities of inorganic osmotic N, P, K^+ , Ca^{2+} , and Mg^{2+} and lower quantities of Na^+ and Cl^- , as well as higher K^+/Na^+ and $\text{Ca}^{2+}/\text{Na}^+$ ratios (Orabi and Abdelhamid 2016). Moreover, they found that the salt-tolerance of the faba bean cultivar "Giza 843" was correlated with a superior capacity of osmotic adjustment by building up proline and P, K^+ , Ca^{2+} , and Mg^{2+} ions, compared to the salt-sensitive cultivar "Giza 3". Many studies have considered tissue Na^+ concentration in NaCl-stressed plants as a

measurement of the mechanism of tolerance (Tavakkoli et al. 2010; Jaarsma et al. 2013; Assaha et al. 2017; Muchate et al. 2019). In parallel, other studies were interested in the high Cl^- concentrations associated with salt tolerance and the Cl^- tolerance mechanism (Teakle and Tyerman 2010; Wu and Li 2019). An experiment was conducted to compare the responses to Na^+ and to Cl^- separately with the response to NaCl in a soil-based system using two varieties of faba bean, that differ in salinity tolerance (Tavakkoli et al. 2010). Consistently with the report of Tavakkoli et al. (2010), they compare the behavior of two faba bean varieties tested under salinity, the variety Nura as salt sensitive and 1487/7 as salt tolerant. The variety 1487/7 exhibited a higher leaf K^+/Na^+ ratio, a significant Na^+ exclusion and better maintenance of leaf K^+ concentrations under Na^+ and NaCl stress compared with Nura. In addition, the variety 1487/7 had a higher leaf osmotic potential as well as a higher photosynthesis rate and higher K^+ and Ca^{2+} concentrations and lower Na^+ concentrations in the shoots. In addition, the variety 1487/7 maintained a higher capacity of the PSII system compared with Nura. Those parameters were proven to be associated with salt tolerance and can be exploited in breeding program for selecting tolerant varieties. There is always a need to develop cultivars, that can tolerate salinity stress. Furthermore, to accelerate breeding cycles, there is a need to use marker-assisted selection, which had not been widely used in legumes.

Genomic tools and plant molecular breeding techniques could accelerate the legume breeding process by understanding plant genetic and genomic (Gnanasambandam et al. 2012; Sallam and UI-Allah 2019). To improve the breeding for salt tolerance in legumes, further identification of stress resistance Quantitative Trait Loci (QTLs) by using comparative linkage mapping is required (Lavania et al. 2014). Several genetic linkage maps have been developed in faba bean in the last decade using bi-parental populations, derived from crosses between two inbred lines (Khazaei et al. 2020). Consequently, two genes *VfWRKY1* and *VfWRKY2* were identified in faba bean and conferred salinity and drought tolerance (Abid et al. 2017). The comparative linkage mapping was also used in field pea (*P. sativum*), where QTLs for salinity tolerance were identified on linkage groups Ps III and VII, with flanking SNP markers suitable for the selection of resistant cultivars (Leonforte et al. 2013). Furthermore, comparative genomic analysis with other legume species showed higher levels of conserved synteny with the genomes of *M. truncatula* Gaertn. and chickpea (*C. arietinum* L.) than with soybean (*G. max* [L.] Merr.), *L. japonicus* L. and pigeon pea (*Cajanus cajan* [L.] Millsp.) QTLs for salinity tolerance were identified on linkage groups Ps III and VII, with flanking SNP markers suitable for selection of resistant cultivars (Leonforte et al. 2013). A genome-wide association study (GWAS) was conducted using a mixed linear

model on 276 accessions of lentil. A range of candidate genes was identified with the most plausible being potassium transporters, which are known to be involved in salt tolerance in related species (Dissanayake et al. 2021). The most marker-trait associations were observed on chromosome 2 as well as chromosome 4. This study also revealed a salt tolerance mechanism in lentils. Tolerant accessions do not transport Na^+ ions around the plant; instead, they are localized within root tissues (Dissanayake et al. 2021). Besides, a SNP-based genome-wide association study to mine genetic loci associated with salinity tolerance was applied in mungbean (*V. radiata* L.) (Breria et al. 2020). SNPs associated with salt-stress tolerance were mostly identified on chromosomes 7 and 9. The associated region at chromosome 7 contains the gene *Vradi07g01630*, which was annotated as ammonium transport protein (AMT). While, the associated region in chromosome 9 contained the genes *Vradi09g0951* and *Vradi09g09600*, annotated as OsGrx_S16-glutaredoxin subgroup II and dnaJ domain proteins respectively and having functions related to salt-stress tolerance (Breria et al. 2020). However, due to the complexity of the genome of some legume species like faba bean, neither QTL mapping nor GWAS were reported earlier for salt tolerance.

Next-generation sequencing (NGS), especially high-throughput RNA sequencing (RNA-seq) technology, one of the most powerful tools currently available for transcriptome profiling can enhance the efficiency and speed of gene discovery in legumes. For example, the RNA-seq method was used to investigate genome-wide transcription profiles of two faba bean varieties with contrasted salt-tolerance during seed germination under salinity (Zhang et al. 2020). A total of 4,486 differentially expressed genes (DEGs) were identified by the comparison of the salt-tolerant variety Y134 and the salt-sensitive variety Y078 treated with salinity or not. Out of these, 1,410 candidate DEGs were identified as salt-stress response genes. Furthermore, 623 DEGs were identified as variety-specific response genes during seed germination at 16 h or 24 h with salt treatment (Zhang et al. 2020). The obtained results are helpful for the understanding of salt tolerance mechanism of crops during seed germination, and provide more genetic resources for future exploitation in faba bean breeding. Another recent example in chickpea, Kumar et al. (2021) utilized a comparative transcriptome analysis of tolerant and sensitive chickpea genotypes in control and salt-stressed conditions. Using Illumina HiSeq-2500, 21,698 differentially expressed genes (DEGs) were identified, of which 11,456 and 10,242 were up- and down-regulated, respectively. They found a significant up-regulation of transcripts encoding potassium transporter family HAK/KUP proteins, MIP/aquaporin protein family, NADH dehydrogenase, pectinesterase, and PP2C family proteins occurred under salt stress. The identification of differentially expressed genes (DEGs) and related pathways by

comprehensive analysis of transcriptomes was also applied in *Phaseolus vulgaris* (Hiz et al. 2014), *Medicago sativa* (Kaundal et al. 2021), *Sophora alopecuroides* (Yan et al. 2020) and *Medicago trunculata* (Zahaf et al. 2012). This will help to understand the salt tolerance mechanism during seeds germination and plant development. The data generated from all the previous studies will accelerate functional and applied genomics research in legumes for their genetic enhancement. Furthermore, it will provide valuable genetic resource for the breeding of salt-tolerant legumes in the future.

Gene manipulation for salt stress tolerance in legumes

While salinity tolerance is a polygenic trait, the breeding approaches in such a case are still very limited, which can explain the scarcity of commercial salt-tolerant crops. Therefore, engineering crops with improved salt stress tolerance traits is one of the most important challenges for modern agriculture (Hanin et al. 2016). Mutagenesis allows the diversification and genetic diversity of plant species (Arriagada et al. 2022). According to the joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculture, a total of 21 mutants of soybean with increased tolerance to abiotic stresses, have been developed to date (<https://mvd.iaea.org/>, accessed on 12 April, 2023). The success of mutagenesis was also reported in other legume species, such as chickpea (Toker 2014), groundnut (Azad et al. 2013), *Clitoria ternatea* (Talukdar 2011), faba bean (El-Awadi et al. 2017) and *Lathyrus sativus* (Talukdar 2011). For example, Toker, (2014) reported an increased tolerance to salt, drought and heat stresses in gamma irradiated *Cicer* species. According to the same author, all the mutant lines displayed a better tolerance to a broad number of abiotic stresses, mainly salinity.

Genetic transformation can also be applied to improve salt tolerance in legume plants (Table 2). For instance, constitutive expression of the pathogenesis-related gene PR10a from potato in transgenic faba bean enhanced plant tolerance to salt stress and osmotic stress (Hanafy et al. 2013). The overexpression of *Arabidopsis* vacuolar Na^+/H^+ antiporter *AtNHX1* in transgenic plants exhibited a higher ability for vacuolar sequestration of Na^+ , maintaining osmotic balance in vacuoles using Na^+ as an ionic osmolyte and reducing detrimental effects of excess Na^+ in the cytosol (Hanin et al. 2016; Kumar et al. 2017). Afterwards, it was also applied to legumes such as alfalfa (Li et al. 2011b), soybean, cowpea (Mishra et al. 2015) and mungbean (Sahoo et al. 2016; Kumar et al. 2017). Recently, *AtNHX1* was transferred into the shoot apices of three Egyptian faba bean cultivars via *Agrobacterium*-mediated transformation. The gene was highly expressed and enhances salt tolerance in transgenic plants (Hassanein et al. 2019).

Transgenic plants overexpressing antioxidants or detoxification molecules such as ascorbate, glutathione, carotenoids, anthocyanins osmolytes, peroxiredoxin and tocopherol can be used to enhance defense in plants (Wang et al. 2003). The transfer of one or several genes that encode for those protecting molecules could be a valuable strategy for increasing salt tolerance. Other molecules could also play a protective role under salt stress. For example, the betaines, proline, mannitol, and trehalose are compatible molecules that may protect plants against salt stress and can act as osmoprotective compounds by directly stabilizing membranes and/or proteins (Slama et al. 2015). A recent study in soybean reported overexpression of a novel *GBI* gene that effectively increased the content of glycine betaine in transgenic plants, which could confer a better tolerance to abiotic stress including salinity (Castiglioni et al. 2018). Always in the soybean, Hoang et al. (2021) reported that transgenic plants overexpressing *GmNAC085* showed a better defense system against salinity-induced oxidative stress, with higher activities of antioxidant enzymes responsible for scavenging hydrogen peroxide or superoxide radicals. Adding that the key stress-responsive of the gene *GmNAC085* is involved in the proline biosynthetic pathway, sodium ion transporter and accumulation of dehydrins. In *M. sativa*, the over-expression of *MsK4* in transgenic plants resulted in the overproduction of sugar metabolism and the accumulation of higher levels of starch and glucose which led to a better tolerance to salt stress (Andersen et al. 2007). Furthermore, the expression of cyanobacterial flavodoxin in transgenic *M. trunculata* induced significant changes in enzymatic activities that involve nodule redox balance, which improved the symbiotic performance under salt stress (Peña et al. 2010). The regulated expression of *AtDREB1A* gene, a class of DREB from *A. thaliana* was studied in transgenic peanut (*A. hypogaea*) lines. The transgenic plants carrying *AtDREB1A* showed improved growth parameters that were correlated with physio-biochemical parameters such as proline content, total chlorophyll content, osmotic potential, electrolytic leakage and relative water content under drought or salinity stress (Sarkar et al. 2014). In addition to the antioxidant defense system, ion transporters and compatible solutes, salinity tolerance mechanism also depend on transcription factors. The transcriptional regulator, *Alfin1*, over-expressed in alfalfa (*M. sativa*) regulates endogenous NaCl -inducible gene expression, resulting in salinity tolerance (Winicov and Bastola 1999). In soybean, the transcription factor-encoding gene *GmMYB84* was modulated by DNA methylation, which confers salinity stress tolerance (Zhang et al. 2020). Similarly, the overexpression of the *GmDREB6* gene improve proline accumulation and salt tolerance in transformed soybean plants (Nguyen et al. 2019b). Although more research is required to identify more genes involved in legume salt tolerance and their expression in transgenic plants.

Genome-engineering using CRISPR-Cas9 technology (clustered regularly interspaced short palindromic repeats-CRISPR associated protein 9) has demonstrated broad potential in developing salt-resilient plants for several plant species (Razzaq et al. 2022). CRISPR-Cas9 offers a precise genetic modification of crops, resulting in a notable increase of varieties obtained in a short period of time. However, few studies have been conducted on legume plants with regard to the improvement of salt tolerance. This advanced technology has mostly been applied in soybean for salt tolerance studies. For instance, the knock-out of *GmA1TR* (ABA-induced transcriptional repressors) genes using the CRISPR/CAS9 genome editing tool to soybean (*G. max*) resulted in better plant growth under saline conditions (Wang et al. 2021). Besides soybean, its silencing in *Arabidopsis* also enhanced salinity and drought tolerance (Chen et al. 2021). CRISPR-Cas9 mediated silencing of *GmNAC06* confers a better salt tolerance to soybean plants (Li et al. 2021). The increased tolerance was associated with a notable accumulation of proline and glycine betaine along with a better regulation of Na^+/K^+ ratio (Li et al. 2021). Salt tolerance has been achieved by overexpressing sodium/hydrogen exchanger *GmHNX5* in soybean, using CRISPR-Cas9 technology. The *GmHNX5* overexpression reduced organelle injuries occurring as a result of salt stress exposure by enhancing the K^+/Na^+ ratio (Sun et al. 2021). At the molecular level, the overexpression of *GmHNX5* was accompanied with an up-regulation of *GmSOS1* and *GmSKOR* genes, encoding for plasma membrane Na^+/H^+ antiporter and sodium/hydrogen exchanger respectively (Sun et al. 2021). With the ability to readily enhance salt tolerance in legume species, genome-editing techniques have the potential to become a powerful tool in crop improvement programs. This is supported by the promising results described above. The CRISPR toolkit is a recent addition to legume study, with a particular emphasis on investigating salinity stress.

Conclusion

Salt stress is one of the major environmental constraints, hampering plant growth, development, and productivity. It negatively affects legume germination and physiology resulting in a significant decrease in plant yield and eventually, plant death. To cope with salt excess occurring in soils and irrigation water, legumes have developed complex mechanisms to overcome the harmful effects of salt stress and to guarantee plant survival and productivity under these growth-limiting conditions. These elaborated mechanisms rely on the involvement of several molecular actors, ensuring stress signal perception, integration, and signaling, leading to the activation of salt response genes by specific transcriptional regulators. Besides the genetic regulation of salt stress

response, epigenetic regulation represents a key component in salt stress response in legume species. An in-depth understanding of the different molecular mechanisms involved in plant response to salt stress undoubtedly facilitates the development of salt-tolerant crops, thereby positively impacting global food security. The comparison between salt-tolerant and salt-sensitive species or cultivars using omics technologies for global molecular profiling (genomics, transcriptomics, proteomics, and metabolomics) offers the possibility to extend our well-understanding of the molecular mechanisms associated with salt tolerance acquisition and thus, developing new strategies for plant breeding for salt-tolerant species. The generated data will hasten/accelerate functional and applied genomics research in legume species for their genetic improvement. Moreover, this will also provide relevant genetic resources for the breeding of salt-tolerance legumes in the future.

Legumes have the great ability to develop synergistic associations with rhizospheric microorganisms, most likely bacteria and arbuscular mycorrhizal fungi, that remain beneficial for plant growth and productivity under optimal and sub-optimal growth conditions. Exploring these worthwhile associations has proven to be one of the most promising alleviation strategies that can be applied to enhance legumes' yield and productivity under salt-stress conditions. Several examples of the great potential of PGPBs and AMF have been addressed in the present review, thereby underlining the possibility of the adoption of bacterial and AMF-derived biofertilizers for sustainable agriculture. However, the scale-up use of these "biofertilizers" in the field represents the only challenge ahead. Seed and plant priming can also be applied to neutralize the negative effects of salt stress on legumes' growth and development. The use of chemical substances such as sodium nitrate, salicylic acid, polyethylene glycol, vitamins, or even low to moderate concentrations of NaCl increases plant survival under salt stress conditions, it has been well-illustrated within this review of the literature. This strategy displays many advantages, mainly the easy implementation and low material requirements compared to the other alleviation strategies. Overall, the different alleviation approaches reviewed above applied alone or in combination with sustainable agriculture practices can be implemented to reduce the deleterious effects of salt stress on legume species and ensure food security worldwide, especially for local populations under the threat of salt excess.

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