Silicon (2022) 14:6517–6534
https://doi.org/10.1007/s12633-021-01466-w

REVIEW PAPER

Exogenous Silicon Application Promotes Tolerance of Legumes and Their N_2 Fixing Symbiosis to Salt Stress

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Received: 20 July 2021 / Accepted: 11 October 2021

Abstract

Legumes, the second-most-important crop family, are a key source of biological nitrogen in agriculture and potentially contribute to sustainable cropping systems. Nevertheless, most legumes are salt sensitive, especially during biological nitrogen fixation (BNF). Therefore, improving legume growth and symbiosis efficiency under this constraint constitutes a great challenge to meet the increasing food demands and to protect soils from negative impacts of chemical fertilizers. In this perspective, silicon (Si) has been found to mitigate salt stress effect and improve legume development at the overall developmental stages. Whether direct or indirectly, Si counteracts salt stress effects on seed germination, plant growth and nodulation. The improvement of water uptake and nutrient homeostasis, the modification of gas exchange, the regulation of phytohormone and compatible solute biosynthesis and the regulation of the antioxidant metabolism under salinity are the key mechanisms evoked by plants upon Si treatment. Furthermore, during rhizobial symbiosis, Si has been shown to induce nodule formation and act on nodule functionality by increasing bacteroids and symbiosomes number, nitrogenase activity and leghemoglobin content under salinity. Here, we reviewed recent progress related to the role of exogenous Si in improving legume salt tolerance and highlighted the mechanisms through which Si could mediate salt tolerance. The needs of future research for better understanding how Si can promote salt tolerance in legumes are also addressed.

Keywords Beneficial element · Salinity · Legumes · Nodulation · Biological nitrogen fixation · Photosynthesis

Highlights

- Silicon (Si) is a beneficial element for enhancing legume plant growth and productivity under salt stress.
- Application of Si improves biological nitrogen fixation by enhancing nitrogenase activity and nodule functionality.
- Si alleviates salt-mediated osmotic stress by up-regulating water uptake and compatible solutes accumulation.
- Si reduces oxidative stress under salinity by activating enzymatic and non-enzymatic antioxidant defense system.
- Si alleviates salt toxicity by regulating nutrient homeostasis.

1 Introduction

Soil salinization and inappropriate irrigation management practices have devastating impacts on legume crops. To date, approximately 20 % of the total arable land is salt-affected [1]. Furthermore, because of the global warming and climatic changes, this threat is predicted to be more severe for the near future [2]. The effect of salt stress on plants including legumes has been comprehensively reviewed and this effect can be observed at overall development stages [3–5]. Indeed, during germination, salinity has been reported to inhibit hydrolytic enzyme activities and to reduce seed reserve mobilization, which in return reduces or completely inhibits seed germination [6, 7]. Salinity has also been reported to reduce leaf area, stomatal conductance, chlorophyll fluorescence and chlorophyll content, which directly reduce the rate of photosynthesis [8–11]. Moreover, the deleterious effect of salt on plants is also mediated through the generation of reactive oxygen species (ROS). At high concentration, ROS were reported to have a damaging effect on cell structure and normal metabolism by

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causing lipids, protein and nucleic acid peroxidation [12, 13]. Salinity reduces legume growth by causing ionic toxicity and nutrient deficiencies [1].

Legumes represent an important source of proteins for both humans and livestocks. Thus, grain legumes are vital component of local diet in developing countries. Likewise, in the agro-ecosystem, legumes play a key role in balancing soil nitrogen (N) content through its biological nitrogen fixation (BNF) with soil rhizobia. This symbiotic interaction limits or reduces the use of chemical fertilizers which are expansive and unfriendly for the environment [14–17]. Legumes are also used in intercropping or rotation with cereals, as the other plants can benefit from the N fixed by theme in symbiosis with rhizobia [18–20]. Moreover, since legumes were demonstrated to be able to reduce greenhouse gas emissions [21], they are widely used in intercropping with cereal, as the intensification of cereal based-cropping system aggravates the greenhouse gas emissions [22]. Additionally, comparing to the monoculture, cereals and legumes have shown higher yield and seed quality when they were cultivated in intercropping [23].

To ensure increase in food demands, it is necessary to increase the global food production by 38 % and 57 % by 2025 and 2050 respectively [24]. Legume species are considered as salt sensitive. Therefore, this imposes more pressure on the use of alternative approaches to maintain food supplies and in the same time on the exploitation of the salt affected land. In this context, the exogenous supplementation of silicon (Si) has been reported to be one of the promising strategies to overcome salt stress effect on plants.

Si, second most abundant element in the earth crust, has got much attention these last few years. It is well documented that Si could improve the plant tolerance to biotic and abiotic stressors [25–28]. Its beneficial effects depend on the plants ability to absorb it from the soil solution. Thus, since some legume species have been characterized as plants without Si transporter, they were considered as Si-rejective [29], which make it difficult to understand how this element improves legumes salt-tolerance. Furthermore, Si should not be considered as essential for plants [26, 29, 30], based on the three criteria of the essentiality of elements established by Arnon and Stout [31]. An element is not considered essential unless (a) its deficiency makes it impossible for the plant to complete its vegetative or reproductive stage, (b) specific symptoms will appear under its deficiency and this can be prevented or corrected only by its supply and (c) it is directly involved in the plant nutrition. Besides, based on the classification of Epstein and Bloom [32], an element should be considered essential if it fulfills either one or both of the following criteria: (a) the element is part of a molecule that is an integral aspect of the plant's structure or metabolism and (b) when compared to plants with lower deficit, the plant can be so severely deficient in the element that it demonstrates anomalies in growth, development, or reproduction. Accordingly, Si will be considered as an essential element for higher plants since its supply confers many physiological and biochemical changes, including plant growth and productivity, photosynthesis, water uptake, nutrient homeostasis, etc. [33–35]. More than that, it has been found that plants without Si tend to grow abnormally showing for example less chlorophyll, leaf senescence and death, growth inhibition and oxidative stress under abiotic stresses, while adding Si helps them to grow up normally [36]. According to Ma et al. [37], Si is the only nutrient that is not harmful when it is excessively accumulated in plants.

Regardless its uptake and being essential in higher plants, exogenous Si has been reported to alleviate salt stress toxicity and to improve seed germination of various plant species including legumes [38]. Furthermore, in salt stressed Mung bean, exogenous Si application increased chlorophyll content, stomatal conductance, transpiration rate, and net photosynthesis [39]. As NaCl caused osmotic stress, applied Si to salt stressed plants induced the accumulation of compatible solutes to counteract water flow from legumes [40–43]. Si application has been reported to increase the activity of some antioxidant enzymes such as ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR) and superoxide dismutase (SOD) and reduced ROS content and lipid peroxidation [42–45]. Thus, although beneficial Si application in improving legume tolerance to some abiotic stresses have been the subject of a couple of reviews these last years [29, 46, 47], the mechanisms by which Si improves legume tolerance to salt stress is steel poorly understood. Here we review recent developments on Si-induced salt stress tolerance in model and cultivable legume species and examines the unreviewed information regarding some morphological and physiological changes in salt-stressed legumes. Mechanisms of detoxifications triggered in salt stressed-legumes under Si treatment are also highlighted. The applications for future research are discussed.

2 Si Uptake, Transport and Accumulation in Higher Plants

In the soil, Si content varies from 50 to 400 g Si Kg^{-1} [33]. Likewise, about 50-70 % of soil mass is SiO_2, which make it the second abundant element, after oxygen, in the earth's crust [48]. However, in contrast to the high abundance of Si in soil, very low amount of Si is available to be directly used by plants because of its low solubility in the soil solution [33, 49]. Generally, all soil grown plants contain Si with an equivalent concentration or more than those of macronutrients (N, P and K) [50]. However, even though all plants were reported to be contained Si in their tissue, the content of plant on it is generally species dependent. It can reach up to 10 % of the total dry weight of plants based on their Si absorption capabilities [51].

According to Handreckt and Jonest [52], plants were classed as high Si accumulator, intermediate or non-accumulator based on their content on Si. However, another classification proposed by Takahashi et al. [53] make possible to group plants into three groups: active, passive or rejective; based on the mechanism by which plant root assimilate Si from the soil solution. In addition, others like Liang et al. [34] and Henriet et al. [54] have reported the coexistence of both active and passive transport within the same plant.

In active accumulators such as sugarcane, rice and wheat, Si accumulation was reported to represent 1.5–10 % of total dry weight of shoots [26]. For other plant species like cucumber and melon described as passive accumulators, their shoots have been reported to contain Si between 0.5 % and 1.5 % of total dry weight [26, 34]. Si content in legume shoots do not exceed 0.5 % of total dry weight [50]. Therefore legumes are classified as Si rejective [29]. However, other authors like Liang et al. [34] and Guntzer et al. [49] have described soybean, a seed legume, as passive accumulator of Si. Likewise, *Vigna radiata* has been recently reported as a Si accumulator [43].

Plant takes up Si from the soil solution in the uncharged form of ortho-silicic acid ($Si(OH)_4$) [30, 55–57], which is present in the soil solution at 0.1 mM to 0.6 mM when pH is below 9 [58]. In addition to $Si(OH)_4$, Zhu and Gong [36] reported that plants could absorb Si from soil solution in the form of SiO_2. It has been widely reported that Si assimilation by plants involved influx and efflux transporters [59], encoded by two genes named *Lsi1* and *Lsi2* respectively [36]. *Lsi1* was shown to encode an aquaporin as an influx transporter [36, 58], which ensures Si transport from the soil solution to the root cells [26]. *Lsi2* encodes a local plasma membrane transporter, which ensures Si movement from exodermal cells to the apoplast [60]. In addition, Ma et al. [58] have also reported that Si translocated to the aerial parts through the xylem using transpiration water flux. Interestingly, based on sequence homology with the rice Si transporter, the model legume *Medicago truncatula* has been reported to have one gene for Lsi1 and one gene for Lsi2, which make this plant a mild Si accumulator [61]. Moreover, recently Nawaz et al. [62] reported that *M. truncatula* have two homologous *Lsi2* genes. Accordingly, *Phaseolus vulgaris* has also been considered as mild Si accumulator, as it also contains one gene for Lsi1 and two genes for Lsi2 [61]. Moreover, Deshmukh et al. [63] demonstrated that soybean assimilate Si through an influx transporter encoded by two genes named, $GmNIP_{2-1}$ and $GmNIP_{2-2}$ and transcriptomic analysis has shown that the expression of those two genes was higher in both roots and shoots. Other legumes such as *Trifolium pretense*, *Vigna unguiculata*, *Glycine max* and *Cicer arietinum* have also been reported to have homologs of *Lsi2* gene [62].

3 The Effect of Exogenous Si on Legume Seed Germination Under Salt Stress

Germination is a critical process in the life cycle of seed plants. This stage is very sensitive to abiotic stressors particularly salinity causing osmotic stress accompanied with ionic toxicity [7]. According to Farissi et al. [64], the effect of salt stress on germination of *M. sativa* seeds was reflected by its delay or its complete inhibition. Only few studies have reported some effects of exogenous Si on legume seed germination under salt stress. For example, Zhang et al. [38] demonstrated that 2 mM of exogenous potassium silicate (K_2SiO_2) improved germination rate, germination index and vitality index of *Glycyrrhiza uralensis* under 150 mM NaCl. Similarly, Alsaeedi et al. [65] showed that 300 mg L^{-1} of nanosilica (NS) is able to increase the final germination percentage and germination speed of *P. vulgaris* seeds by 19.7 % and 22.6 % respectively under 5 g Na^+ L^{-1} and vigor index by 144.6 % under 4 g Na^+ L^{-1}. The authors also showed that germination time was decreased from 6.43 under 4 g Na^+ L^{-1} to 5.83 when the seeds were treated with 300 mg L^{-1} of NS, reflected 9 % of reduction. Otherwise, priming of *Triticum aestivum* L. seeds with 30 mM of sodium silicate (Na_2SiO_3) restored seed germination to 100 % under 120 mM NaCl [66]. In the same line, *Lactuca sativa* L. seed priming with 0.1 mM of calcium silicate (Ca_2SiO_4) has been recently reported by Alves et al. [67]. Authors found that Si mediates seed germination under 50 mM NaCl highlighted by high germination percentage and germination rate index. According to Biju et al. [68], Si improves lentil seed germination under drought stress through an increase of hydrolytic and antioxidant enzymatic activities. In addition, as seed germination is modulated by gibberellic acid (GA) / abscisic acid (ABA) ratio [69, 70], Si has been reported to mediate *Cucumis sativus* L. seed germination under high level of salt stress (up to 250 mM NaCl) by inhibiting the expressing of *GA20ox* catabolism gene as well as those responsible for ABA anabolism such as *NCED1* and *NCED2* [71]. However, mechanisms by which Si-mediated legume seed germination under salt stress is still poorly understood and detail studies under these conditions are needed for better understanding the mechanism by which Si improves this key process.

4 Effect of Si on Growth, Biomass and Yield of Legumes Under Salt Stress

Legumes are cultivated mainly for forage or grain production. Because they are salt sensitive, their biomass under salt stress is severely affected, particularly when their growth depends on BNF. Improving legumes growth and productivity by using alternative approach under abiotic stresses is of such interest. Si was shown to enhance plant growth at different agronomical, morphological and physiological levels [72]. In *M. sativa*, Meng et al. [73] tested the effect of 2 mM Na_2SiO_3 supplementation to the soil solution on 200 mM NaCl tolerance. They found that exogenous Si can mitigate the adverse effect of NaCl on *M. sativa* growth by greater shoot and root dry weight by 16 % and 11 % respectively. Similar results have been found by Lee et al. [74] on *G. max*, where the addition of 2.5 mM Na_2SiO_3 under 80 mM of NaCl significantly increased shoot and root lengths, plant fresh weight and plant dry weight by 18 %, 11 %, 33 % and 9 % respectively relative to salt-stressed plant without Si supplementation. Furthermore, in salt-stressed cowpea and kidney beans, 1 mM $CaSiO_3$ improved root dry weight, stem dry weight, shoot dry weight and whole plant dry weight in the two evaluated plant species [75]. Wu et al. [42] found that 1 mM Na_2SiO_3 could alleviate *Onobrychis viciaefolia* damage caused by 100 mM NaCl and improve plant fresh and dry weight as well as the number of leaves. In addition to the number of leaves, Si was also found to be able to delay the premature leaf senescence under abiotic stresses including salt stress [8]. Moreover, adding 4 mM of K_2SiO_3 to *C. arietinum* was found effective in alleviating the negative effects of salt on shoot dry weight, root dry weight and seed yield [41]. In the same plant species, 0.5 or 1 mM of exogenous Na_2SiO_3 has been confirmed to be able to increase grain yield under salt stress [76]. In the line with this, foliar spray of diatomite to *Vicia faba* alleviated the negative effect of salt and improved pod number, pod dry weight, seed number and seed dry weight and the effect was more obvious when Si was applied at 1000 ppm [77]. In a similar study conducted by Kardoni et al. [78] on *V. faba*, Na_2SiO_3 counteracted the negative effects of a wide range of salt treatment (1, 2, 3, 4 and 5 ds m^{-1}) and improved grain yield and 100-seed weight. Adding Si to salt-stressed *P. vulgaris* resulted in an increase of seed number, 100-seed weight and yield [79]. Above findings strongly suggested that depending to the form of applied Si and the severity of stress, exogenous Si increased legume plant growth and productivity under salt-induced stress (Fig. 1).

5 Si Balances Legume Minerals Uptake Under Salty Conditions

Salinity has devastating impacts on legume plant nutrient uptake. As mineral nutrient uptake plays an important role in plant development, maintaining ion homeostasis by regulating their uptake, transport and translocation is essential for plant not only to survive under salt stress but also to continue its growth, development and productivity [4]. Investigations on the effect of exogenous Si on plant nutrition has revealed its crucial role in restoring ion homeostasis under salt stress, as observed in several forage and grain legumes plant species [47]. In *C. arietinum*, Garg and Bhandari [41] reported that 0.4 mM K_2SiO_3 application increased the accumulation of each of N, P, Mg and K contents under salt stress. Accordingly, Si application increased the content of salt stressed *T. alexandrinum* on K, Ca, Mg and P by 46 %, 56 %, 45 % and 70 % respectively as compared to the Si-untreated stressed plants. Similarly, in a study conducted by Hellal et al. [77] on *V. faba*, the content of P and K in both shoot and seed were gradually decreased as salt increased in soil solution, but SiO_2 application as foliar spray reduced this effect. Furthermore, 1 mM of K_2SiO_3 improved the tolerance of *M. sativa* to 120 mM NaCl and increased Ca^{2+} content in roots and Mn^{2+} content in leaves [80]. Increased uptakes of K^+ and Ca^{2+} following application of Si were also reported in salt-stressed cowpea, kidney bean [75] and in *V. radiata* [43].

Mechanisms by which exogenous Si could increase soil P availability and its uptake by plants include (i) a decrease in P sorption in soil [81] (ii) a better Pi uptake by roots by increasing root exudation of some organic acids like malate and citrate [82], (iii) an increase in soil P availability by augmenting soil pH [81], (iv) and upregulation of some plant genes involved in P uptake particularly during P starvation [82].

The above studies strongly suggested that exogenous Si alleviates salt stress in legumes by improving uptake of some nutrients. However, for better understanding the mechanisms involved in this process, studies on some enzymes involved in nutrient assimilation such as nitrate reductase, phytase and phosphatase as well the regulation of their expression are essential to get a better understanding of the Si effect.

6 Exogenous Si Maintained Plant Water Balance in Salt-stressed Legumes

Reduction of leaf relative water content (RWC) is one, among other, of the most physiological traits that serve as an osmotic stress index [33]. Si has been reported to be able to maintain RWC in plants growing in saline environments [40, 83–85]. In 4.5 g SiO_2 Kg^{-1} soil treated-*T. alexandrinum*, RWC was raised in the salt-sensitive genotype from 62.40 to 81.03 % in the presence of 3000 ppm NaCl indicating an improvement rate of 32 % of RWC [86]. In contrast for the salt-tolerant genotype, the improvement rate was only 17 %. In addition, Mahmood et al. [39] found that RWC was 1.37- and 1.44-fold higher in salt-stressed mung bean treated respectively with either 1 or 2 kg K_2SiO_3 ha^{-1} as a foliar spray than in the absence of Si. In the same line, 4 mM K_2SiO_3 significantly alleviated the negative effect of 100 mM NaCl stress raising RWC in both salt-tolerant-HC 3 and salt sensitive-CSG 9505 genotypes of *C. arietinum* [41]. In the same way, 0.6 g K_2SiO_3

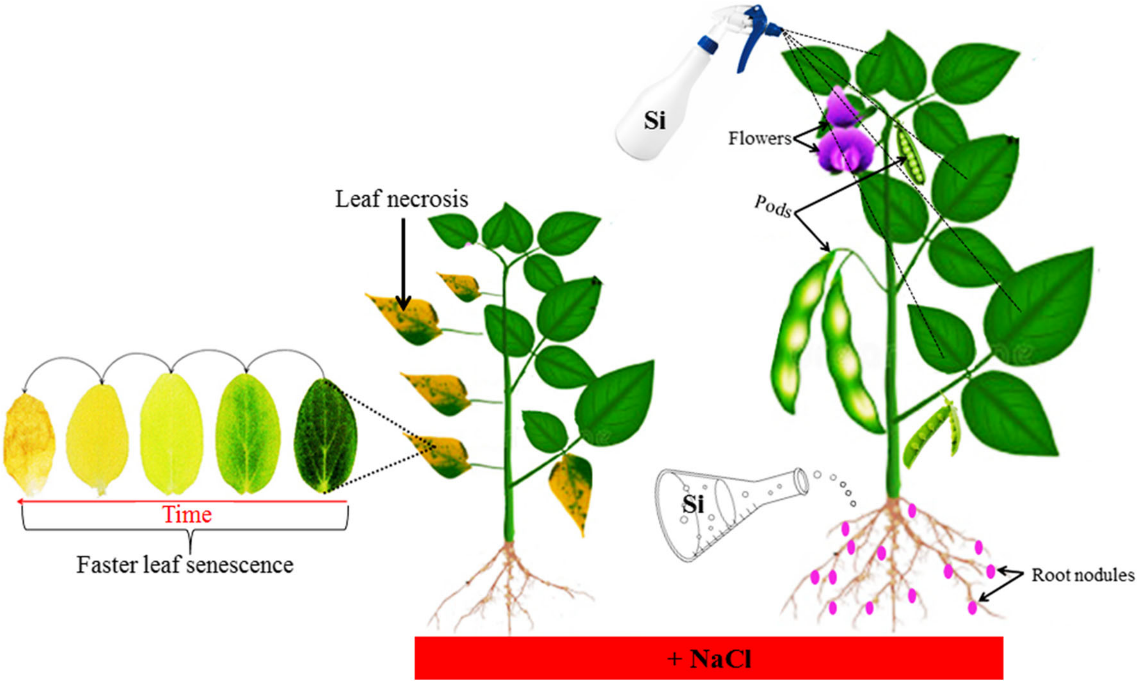

Fig. 1 Proposed effects of exogenous silicon treatment on legume plants growth and productivity under salt stress conditions. Abbreviations: NaCl, sodium chloride, Si, silicon

kg^{-1} soil increased the RWC and reduced the leaf water potential in two-year-old *G. uralensis* plants under different salt concentrations (6 and 9 g NaCl Kg^{-1} soil) and after different time of treatment [87]. Improving plant RWC under salt stress after Si supplementation has also been documented in *V. radiate* [43].

Maintaining water content under osmotic stress is a complicated process resulting from a balance between water uptake and water loss by transpiration. According to Zhu and Gong [36], silicic acid polymerizes and precipitates forming an opal phytolith that prevents water loss. Similarly, Coskun et al. [26] documented that Si prevents water loss under osmotic stress by its deposition in cuticles. On other hand, Si has been reported to modulate aquaporin-related gene expression, which is particularly important to improve water homeostasis and balance particularly under water stress [88]. Furthermore, Si could improve cellular osmotic potential through synthesis of compatible solutes (See Section 7). Studies behind these findings are still needed particularly at the molecular level for better understanding the possible mechanisms induced by Si to mediate osmotic stress tolerance.

7 Exogenous Si Mediates the Biosynthesis of Compatible Solutes in Salt-stressed Legumes

Osmotic adjustment through the accumulation of compatible solutes is one of the adaptive salt-tolerance strategies adopted by legumes particularly during N_2-fixing process [89]. Indeed, sucrose, fructose and glucose contents were increased by 20–30 % in root of 100 mM salt-stressed *Onabrychis viciaefolia* plants when treated with 1 mM Na_2SiO_3 as compared to salt-stressed control plants [42]. Likewise, in *G. uralensis*, Zhang et al. [87, 90, 91] reported an increase in the content of soluble sugars as a response to Si addition under salt conditions. In the same way, Ahmad et al. [43] documented that Si improved *V. radiata* salt stress tolerance by an increase in glycine betaine content. According to Garg and Singh [92], exogenous application of K_2SiO_3 was also able to modulate trehalose metabolism in pigeon pea nodules by on the one hand improving trehalose 6-phosphate synthase and trehalose 6-phosphatase activities and on the other hand inhibiting the activity of trehalase, which results in high nitrogenase activity, leghemoglobin and N content under cadmium (Cd) and zinc stresses.

Proline accumulation is recognized as a tolerance index because its concentration has been shown to be generally higher in salt tolerant than in salt sensitive plants. However, toxic effects of proline when applied exogenously have been reported [93]. According to Zhang et al. [90, 91], treatment of salt-stressed *G. uralensis* by Si led to the accumulation of proline. Similarly, *V. radiata* and *O. viciaefolia* plants exposed to salt stress have higher proline contents when treated with exogenous Si [42, 43]. In contrast, applied 4.5 g SiO_2 Kg^{-1} soil to salt stressed *T. alexandrium* plants resulted in lowering proline content by 26 % as compared to Si untreated salt-stressed *T. alexandrium* plants [86]. Moreover, in a study carried out by Lee et al. [74], the authors found that the application of $CaSiO_3$ at 2.5 mM to the soil solution of 80 mM NaCl-stressed *G. max* reduced proline content as compared to Si-untreated salt-stressed plants. Negative correlation between Si addition and proline content was also reported by Mahmood et al. [94] and Zamani et al. [76] in salt stressed Mung bean and *C. arietinum* respectively.

Above studies clearly indicate that Si might enhance salt tolerance in legumes by involving osmolytes production and provide the evidence that Si plays a crucial role in osmotic adjustment.

8 Si-mediated Biosynthesis of Phytohormones in Salt-stressed Legumes

Phytohormones are compounds produced in very low concentrations but able to regulate a variety of cellular processes and plant responses to changing environmental conditions including salinity [95, 96]. For example, excessive concentrations of some ions like Na^+ and Cl^- have been shown to induce a change in the endogenous level of plant growth hormones [97]. It was shown that salt stress increases the level of ABA in *P. vulgaris*, which inhibits the transport of both Na^+ and Cl^- to the shoot [98]. In *G. max*, Lee et al. [74] showed an increase in ABA level under 80 mM NaCl conditions, however when exogenous Si was applied, a lower ABA content was measured. Similar results were also reported by Zhang et al. [87] on *G. uralensis*. The authors demonstrated that K_2SiO_3-treatement contracted the effect of NaCl on ABA and decreased its endogenous level. In addition, exogenous application of GA was found to be useful to contract the devastating impact of salt stress on *V. radiate* [99]. In this line, Lee et al. [74] tested the effect of 2.5 mM Na_2SiO_3 treatment on *G. max* tolerance to 80 mM NaCl through GA regulation. Results indicated that GA_1, GA_4, GA_{12}, GA_{19} and GA_{24} levels were decreased upon salt stress, while the supplementation of Si significantly increased their levels. In a similar study, applied K_2SiO_3 mediated *G. uralensis* salt tolerance by increasing GA_3 level [87]. Indolacetic acid (IAA) accumulation has also been reported as one of the key responses of salt tolerance [96], and its exogenous application has been recommended as a crucial strategy to alleviate the adverse effect of salt on plants [100]. In *G. uralensis*, Zhang et al. [87] demonstrated that IAA was decreased upon salt stress but increased in response to Si treatment.

9 Exogenous Si Improves Photosynthesis in Legumes Under Salt Stress Conditions

Salinity was found to reduce leaf area and gas exchange as well as chlorophyll synthesis leading to a decrease of photosynthesis and as a result plant growth and productivity [4, 10]. Si has been largely reported to have positive effects on plant growth under changing environments and these effects have been confirmed to be often associated with the ability of Si to improve photosynthesis [47, 101]. Mahmood et al. [39] conducted a study on mung bean exposed to salt stress, and they found that spraying K_2SiO_3 (1 and 2 kg ha^{-1}) on 10- and 30-day-old plants importantly resulted in higher net photosynthesis, chlorophyll and carotenoids contents, stomatal conductance and transpiration rate compared to untreated salt-stressed control. In a similar study conducted recently by Meng et al. [73], 2 mM Na_2SiO_3 supplementation to *M. sativa* was found to mitigate the inimical impact of 200 mM NaCl by increasing various photosynthetic attributes including chlorophyll content, net photosynthesis, stomatal conductance and transpiration rate. In addition, after one month of 60 mM NaCl treatment, leaf area, stomatal conductance and net photosynthesis were increased respectively by 26 %, 37 % and 28 % in *P. vulgaris* plants when they were treated exogenously by 1.5 mM K_2SiO_3 [102]. Under salt conditions, Si was also reported to increase stomatal number and improves RuBisCO activity and as a result internal CO_2, which supports a key role of Si in photosynthetic activity [41, 43, 75]. Beneficial effects of Si on chlorophylls under salt stress has been studied by Alamri et al. [8] in *Brassica juncea*. They found that Si could increase the activity of some chlorophyll synthesis enzymes including δ-aminolevulinic acid dehydratase and porphobilinogen deaminase and inhibits those responsible on its degradation, such as chlorophyllase, chlorophyll-degrading peroxidase and pheophytinase. The roles of Si on photosynthesis indexes in salt-stressed legume plants are summarized in Table 1.

10 Biological Nitrogen Fixation is Enhanced by Si Under Salt Stress Conditions

BNF in legumes has proved in many studies to be limited under salt stress, because of the high salt sensibility of nodulation process and nitrogenase activity [106, 107]. Exogenous Si application has been reported as one of the most effective strategies to improve legumes nodulation and N_2 fixation particularly under stressed conditions [46, 47]. Indeed, improving BNF by exogenous Si under salt stress has been shown by Kurdali et al. [108] on *Sesbania aculeata.* An increase of 39 % of the amount of N fixed was noted in plant treated with

Table 1 Roles of exogenous Si in legume photosynthesis improvement under salt stress conditions

Legume species	Substrate	Salt stress		Exogenous silicon			Specific functions	References
		Level	Duration (day)	Form	Application way	Level		
Cicer arietinum	Sand : loam	60, 80 or 100 mM	65	K_2SiO_3	Growth solution	4 mM	Increased total Chl and RuBisCo activity.	[41]
Cowpea	Hydroponic conditions	40 mM	Not shown	$CaSiO_3$		0.5 or 1 mM	Increased Pn, E, gs, Ci and total Chl.	[75]
Glycyrrhiza uralensis	Field conditions	3.12, 5.46 or 7.81 dS m^{-1}	Not shown	K_2SiO_3	Foliar spray	1 or 2 kg ha^{-1}	Increased Chl a, gs, E.	[39]
	Sandy loam soil	6 g Kg^{-1}	90 70 and 110		Add to the soil	0.1 g Kg^{-1}	Increased Pn, E and gs. Increased Chl a, Chl b, Chl a+b and Chl a/Chl b ratio.	[103]
Glycine max	Hydroponic conditions	100 mM	1 and 2	Not shown	Growth solution	2 mM	Increased total Chl, Ci, gs, E, Pn, Pn/Ci ratio and Pn/E ratio.	[104]
Kidney bean		40 mM	Not shown	$CaSiO_3$		0.5 or 1 mM	Increased Pn, E, gs, Ci and total Chl.	[75]
Medicago sativa	Soil	50, 100 or 200 mM	28	Na_2SiO_3		2 mM	Increased Chl, Pn, gs and E.	[73]
Phaseolus vulgaris	Peat: vermiculite	30 or 60 mM	23 and 30	K_2SiO_3		1.5 mM	Increased gs and Pn.	[102]
	Ion-free sand	150 mM	30		Foliar spray	6 mM	Increased Pn, E, Chl a, Chl b and carotenoids.	[105]
Trifolium alexandrium	Soil	2000 or 3000 ppm	75	SiO_2	Growth solution	1.5, 3 and 4.5 g Kg^{-1}	Increased Pn and total Chl.	[86]
Vicia faba		2.84, 6.03 or 8.97 dS m^{-1}	45 and 90		Foliar spray	250, 500 or 1000 ppm	Increased Chl a, Chl b and carotenoids.	[77]
Vigna radiata	Sand : vermicompost	50 or 100 mM	29	Na_2SiO_3	Growth solution	2 mM	Increased FS, Chl a, Chl b, Total Chl, Carotenoids, Fv/Fm, QPSII, qp, NPQ, A, E and gs.	[43]

Abbreviations: A, CO_2 assimilation; Chl, chlorophyll; Ci, intercellular CO_2; E, transpiration rate; FS, frequency of stomata; NPQ, non-photochemical quenching; Pn, net photosynthesis both NaCl and Si as compared to salt stressed control. Additionally, using the acetylene reduction assay, Putra et al. [109] found that the activity of nitrogenase in *M. truncatula* root nodules was boosted by more than 85 % upon Si-treatment, which potentially reflects an increase in N fixation mediated by rhizobia. Similarly, under cadmium and zinc toxicity, exogenous application of 300 mg K_2SiO_3 kg^{-1} soil to *Cajanus cajan* resulted in an increase of nodule number, nitrogenase activity, leghemoglobin concentration and as a consequence an increase of N content [92]. Furthermore, applied Si to the unstressed *G. max* (BRS- MG 800 A cultivar) resulted in an increase of the root nodule number, nodule size and leaf N content by 82 %, 38 % and 18 % respectively when compared to Si-untreated plants [110]. Similarly, in *V. unguiculata*, Nelwamondo and Dakora [111] reported that Si promotes nodule formation as well as their function. According to Putra et al. [46], improved nodule activity in response to Si application might be related to the ability of Si to accelerate exchanges of solutes and gasses between the soil and the plant. In addition, Si has also been reported by Nelwamondo et al. [112] to have a positive structural effect inside nodules by increasing the number of bacteroids and symbiosomes. Studies also reported that Si accumulates in nodules and increases cell wall thickness [46]. Si-increased nodulation could be explained by the increase of the infection sites [108, 113]. Another explanation of the increased number of nodules upon Si treatment is the fact that silicification might affect some key symbiotic signals such as flavonoid compounds required for symbiosis establishment [46, 114]. More interestingly, by analyzing rhizospheric soil of *G. max* plants, Shamshiripour et al. [115] indicated that Si has also the potential to increase populations of bacteria such as silicate-solubilizing bacteria population as well as microbial biomass and respiration rate. The above studies suggested that exogenous Si may represent an effective strategy to improve BNF under salt stress (Fig. 2), but detail mechanisms are still not clear.

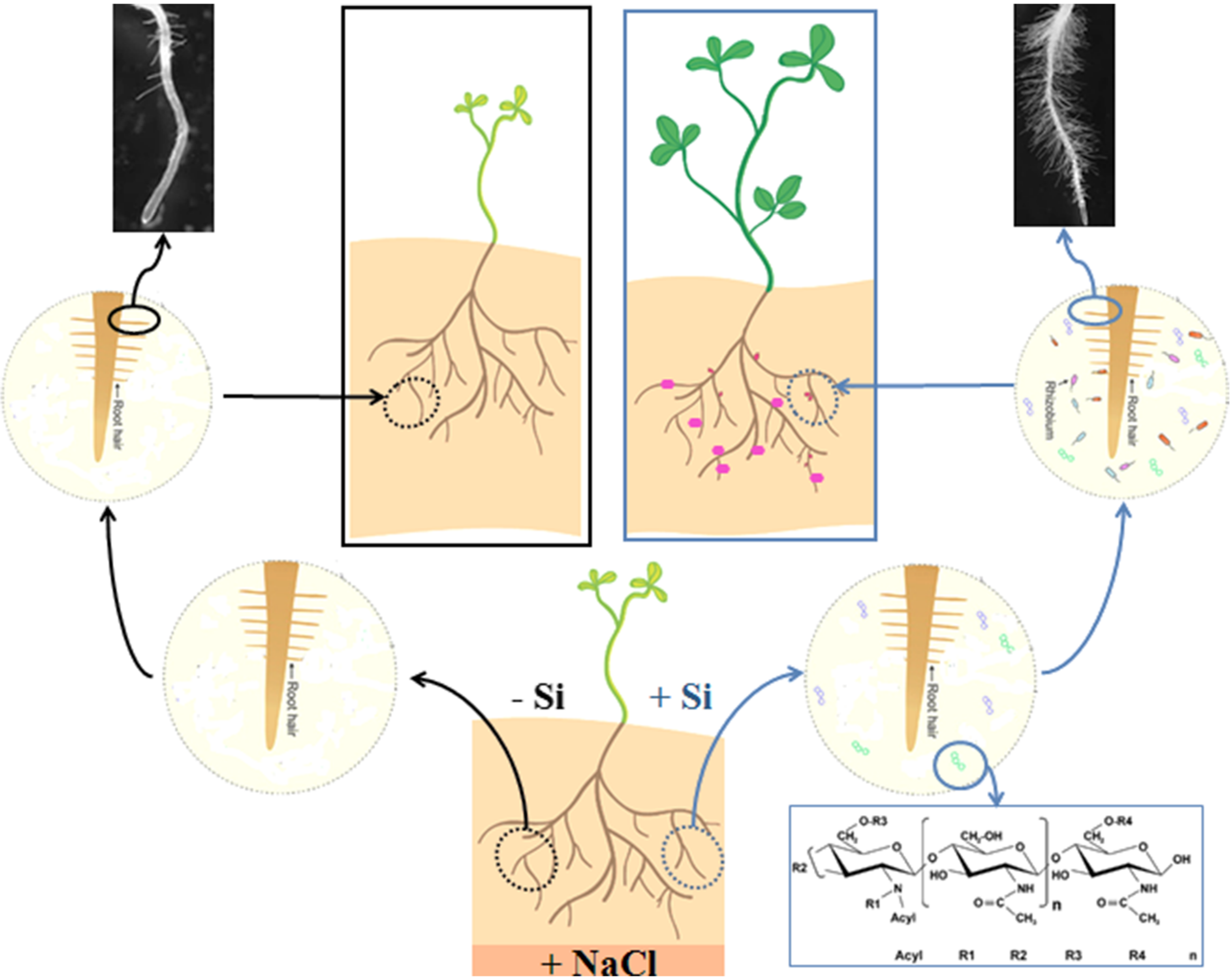

Fig. 2 Proposed representation of how does silicon (Si) treatment promote legume root nodulation under salt stress. Si addition modulates isoflavonoids secretion involving in free-living rhizobia attraction which in return secrete some biochemical substance (Nod factors) leading to root nodulation

11 Exogenous Si Reduces Ion Toxicity in Legumes Under Salt Stress Conditions

Decrease of the Na^+ uptake and/or its sequestration into vacuole represent a crucial adaptive strategy used by plants to increase their tolerance to salt stress [116]. When *C. arietinum* was treated with exogenous K_2SiO_3, a decrease in Na^+ uptake was observed leading to an increase of K^+/Na^+ ratio [41]. In the same line, Shahzad et al. [117] showed in *V. faba* that 1 mM Na_2SiO_3 was able to reduce leaf Na^+ content by 22 % and Cl^- by 14 % with an increase in K^+/Na^+ ratio. Similarly, when applied exogenously to salt stressed plants, Si induced a decrease of Na^+ and an increase of K^+ in shoot and leaves of *M. sativa* and of *T. alexandrinum* as compared to salt-stressed plants [80, 86]. Recently, Zhang et al. [91] presented a key role of Si in the reduction of salt toxicity in *G. uralensis* by reducing the Na^+ uptake and increasing K^+/Na^+ ratio. In *V. unguiculata* and *P. vulgaris*, Murillo-Amador et al. [75] showed a low shoot/root Na^+ ratio for both species. Furthermore, in *P. vulgaris*, Zuccarini [102] reported that Si reduced Na^+ in the leaves more than in the roots. These results demonstrate that Si not only reduced the uptake of Na^+ by roots, but also its translocation to aerial parts.

Several studies have reported a key role of the Na^+/H^+ antiporter in maintaining Na^+ homeostasis under salt stress by sequestrating it in vacuole or its exclusion from the cytosol [36, 89]. Two Na^+/H^+ antiporters were reported, SOS1 localized in the plasma membrane and NHX in the tonoplaste [72]. In salt-stressed *Zea mays*, 1.5 mM of exogenous $Si(OH)_4$ upregulated both *SOS* and *NHX* transcript levels under 40 mM NaCl and decreased root Na^+ content [118]. As K^+/H^+ symporter plays an important role in maintaining K^+ homeostasis, Si was also reported to increase the activity of this symporter under salt stress, which increases K^+ content in plants helping to maintain osmotic homeostasis [119]. These findings could explain the fact that Si decreased Na^+ and Cl^- and increased K^+ in salt stressed legumes (Fig. 3).

Contrary to the above studies, Romero-Aranda et al. [83] reported that 2.5 mM K_2SiO_3 application has no effect on Na^+ and Cl^- contents in NaCl-stressed *Lycopersicon esculentum*. These results showed that Si-reduced osmotic stress under salinity does not always depend on the effect of Si in reducing Na^+ and Cl^- contents. In the other hand, Si-mediated osmotic adjustment by inducing compatible solute biosynthesis under salt stress (See Section 7) is one of the most important strategies to cope with salinity-mediated osmotic stress. In the line with this, the addition of 2.5 mM K_2SiO_3 to the soil solution of salt stressed-*L. esculentum* plants resulted in a decrease of leaf water potential leading to an increase in plant water content [83]. Similarly, Tuna et al. [84] showed a better relative water content in leaves of salt-stressed barley with Si treatment. Si

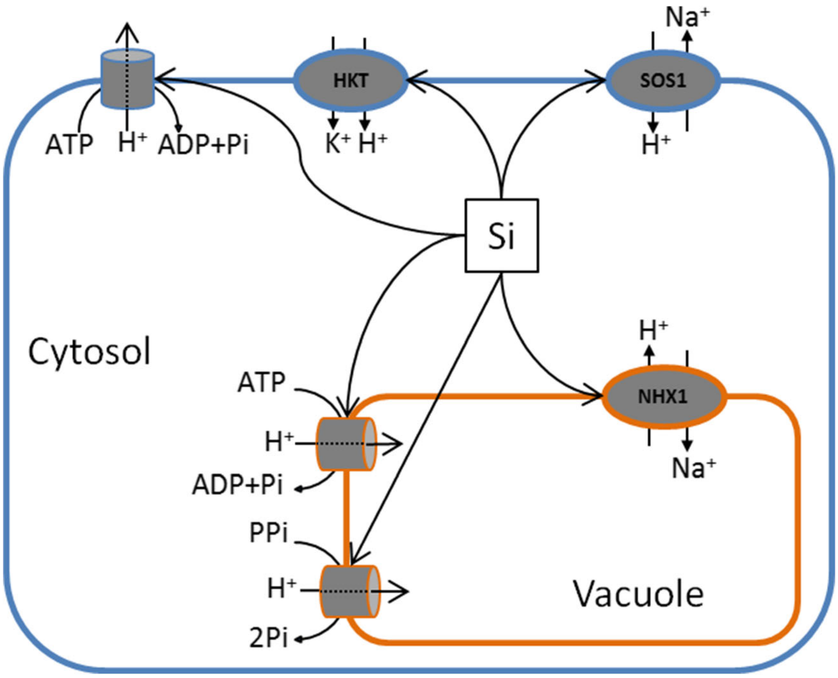

Fig. 3 Proposed mechanisms of the action of silicon (Si) in the reduction of salt toxicity in legumes. Abbreviations: Si, silicon; SOS1; salt overly sensitive 1; HKT, high-affinity K^+ transporters; NHX1, sodium/hydrogen exchanger 1

increased plant water content under salt stress could explain the important role of Si in improving salt tolerance by diluting salt concentration in the cells.

12 Exogenous Si Reduced ROS Production and Membrane Damage in Salt-stressed Legumes

Salt stress triggers ROS accumulation, leading to an oxidative stress and membrane damage [13]. Malonyldialdehyde (MDA), reflecting membrane lipid peroxidation, is widely used as an oxidative stress and membrane integrity indicator [44, 120]. Incorporation of 2 mM Na_2SiO_3 to the growth medium of salt-stressed *M. sativa* (50-200 mM) significantly reduced leaf contents of superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2) and MDA [73]. In *T. alexandrinum*, SiO_2 increased membrane stability index from 62.4 to 80.9 in helaly cultivar and from 74.3 to 82.6 in Sarw1 cultivar under severe salinity stress (3000 ppm) [86]. Similar findings were reported by Mahmood et al. [39] who showed that electrolyte leakage was reduced by 24 % in salt-stressed mung bean as a response to 2 kg K_2SiO_3 ha^{-1} applied as a foliar spray. Likewise, exposure of *G. uralensis* to NaCl increased MDA content and membrane permeability in plants after 150 days of treatment and this was found to be mitigated by 0.6 g K_2SiO_3 Kg^{-1} soil supplementation [87]. The same was found by Wu et al. [42] in *O. viciaefolia* treated with 1 mM Na_2SiO_3 under 100 mM NaCl. Exogenous Si-mediated membrane stability under salt stress was also reported in *V. radiata* [43], Cowpea and kidney bean [75].

13 Exogenous Si Reduces Oxidative Stress in Salt-stressed Legumes

Under abiotic stress, plants set up various non-enzymatic and enzymatic mechanisms to detoxify the excess of ROS. Studies showed that Si could alleviate salinity-induced oxidative stress by increasing the content of non-enzymatic scavengers such as ascorbic acid (AsA), alkaloids, flavonoids and carotenoids and by inducing the activity of enzymatic systems including superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR) and glutathione S-transferase (GST) [72, 121]. Indeed, Meng et al. [73] reported that exogenous application of 2 mM Na_2SiO_3 to the growth medium of *M. sativa* exposed to 200 mM NaCl for 28 days significantly decreased the content of H_2O_2 and O_2^- and this decrease was significantly correlated with an increase in SOD, peroxidase (POD) and CAT activities. Zhang et al. [91] showed that K_2SiO_3 addition to *G. uralensis* treated with NaCl for 110 days reduced O_2^- and H_2O_2 content, increased some non-enzymatic antioxidants like AsA and glutathione (GSH) as well as activities of some antioxidant enzymes such as APX, CAT, GPX and POD. Similar findings have been documented by Zhang et al. [90] on the same plant species, where AsA and GSH contents was increased and the activities of APX, SOD, POD and CAT were improved by 1 mM of K_2SiO_3 under 100 mM NaCl treatment. In addition, in a study conducted by Wang et al. [45] on 120 mM NaCl-treated *M. sativa*, supplementation of 1 mM K_2SiO_3 to the growth medium significantly increased the activity of APX in roots, shoots and leaves. In the same work, the authors showed an increase in the activities of CAT and POD in leaves and shoots respectively. In agreement with these results, Ahmad et al. [43] reported an increase in the activities of SOD, CAT, APX and GR in *V. radiata* as a response to salt stress induced by 100 mM NaCl application and these enzymatic activities were further boosted in salt-stressed plants when they were treated with 3 mM of exogenous Na_2SiO_3. These studies highlithed that Si could reduce oxidative stress in legumes under salinity by inducing both enzymatic and non-enzymatic antioxidant activities (Fig. 4; Table 2). In addition to these findings, studies on antioxidant related gene expression in response to Si application particularly under abiotic stress would be interesting for better understanding of the mechanisms by which Si-mediated oxidative stress tolerance in legumes.

14 Effect of Si Fertilizers Under Field Conditions

Previous investigations evidenced the positive effects of Si on plant growth and productivity, and especially under changing environments [25]. However, the majority of studies have been conducted greenhouses under controlled conditions, which may not reflect the effect of Si under field conditions. For example, to improve the tolerance of *Z. mays* to Cd stress under field conditions, Wang et al. [124] used different Si forms including Si-calcium (CaSi), Si-potash (KSi), semi-finished product of Si-potash (SKSi) and Na_2SiO_3 fertilizers. Here the authors demonstrated that 9000 kg CaSi ha^{-1}, 900 kg KSI ha^{-1} and 900 SKSi ha^{-1} reduced Cd concentrations in plants by up to 71.5 %, 42 % and 40.7 % respectively compared with the control. Conversely, as compared to control, Na_2SiO_3 induced a slight increase in plant Cd concentration, which impaired *Z. mays* plants growth. However, in another interesting study conducted by Taha et al. [125] in *T. aestivum* grown in salt-stressed soil, 30 mM Na_2SiO_3 foliar spray increased significantly plant growth, photosynthesis,

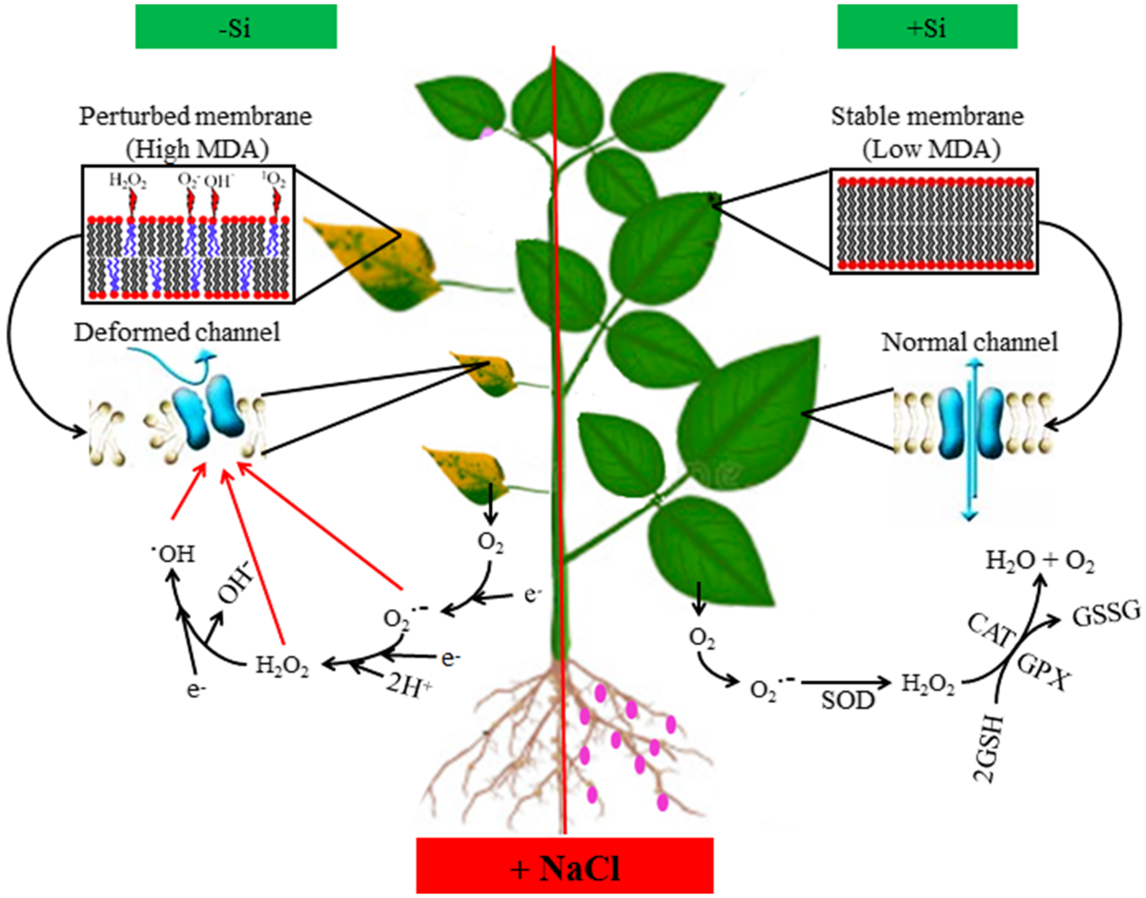

Fig. 4 Schematic overview of Si-mediated oxidative stress regulation in legume plants under salt stress condition. Salt stress induced an overproduction of reactive oxygen species (ROS) leading to a loss of membrane integrity, while Si addition helps in ROS scavenging by increasing antioxidant enzymes activities. Abbreviations: Si, silicon; MDA, malonyldialdehyde; O_2, oxygen; e-, electron; $O_2^{\cdot -}$. superoxide anion; H^+, proton; H_2O_2, hydrogen peroxide; $^{\cdot}OH$, hydroxyl radical; SOD, superoxyde dismutase; CAT, catalase; GPX, glutathione peroxidase; GSH, reduced glutathione; GSSH, oxidized glutathione; NaCl, sodium chloride

performance index, membrane stability index, RWC, compatible solutes and enzymatic and non-enzymatic antioxidants system. In addition, using 150 mg $CaSiO_3$ kg^{-1} soil, as a sustainable strategy, improved significantly plant height, number of tillers, number of grains per spike, 1000-grain weight, harvest index and K^+/Na^+ ratio of *T. aestivum* grown in salt-affected soil [126]. Moreover, when sprayed on the leaves at a rate of 2 kg ha^{-1}, K_2SiO_3 increased stomatal conductance, transpiration rate, RWC, photosynthetic pigments, and salt tolerance index, alleviating as a result the negative effects of salinity on *V. radiata* growth and production [39]. Similarly, when applied exogenously at 300 kg ha^{-1}, Si fertilizer (with 62.9 % of SiO_2) improved *O. sativa* tolerance to water stress and the effect was dose and timing dependent [127]. In the line with these results, application of K_2SiO_3 at the rate of 12 kg ha^{-1} resulted in a higher yield and biomass in *T. aestivum* plants grown under drought stress [128]. Likewise, in a calcareous grey desert soil, SiO_2 supplementation to the plow layer (20 cm in depth) at the rate of 600 kg ha^{-1} increased both yield and fruit quality of table *Vitis vinifera* [129]. More interestingly, since 2014, about 13 field trials have been conducted in Morocco in sugar beet treated with Agrisilica (26 % of Si) fertilizer during sowing at doses of 150, 200, 250, and 300 kg ha^{-1} [130]. Results indicated that sugar beet yield was systematically increased up to 40 % with the increase of fertilizer dose, and an increase in the sugar yield by 4.8 Mg ha^{-1} was observed when Si fertilizer was applied at 250 kg ha^{-1}. Moreover, $CaSiO_3$ supplementation to the growth medium or K_2SiO_3 foliar spray were reported to reduce *Phakopsora pachyrhizi* pathogenesis in *G. max* by 43 and 36 % respectively [131]. Si fertilizers were also reported to improve growth and productivity of other crops including corn, rapeseed, potato, meadows, berry, vegetables, orchards and ornamental plants under both normal and stressed conditions [132]. Above studies clearly indicated that Si could be used as a fertilizer to improve crops growth and productivity under field conditions, and the effect is depending to the form, the optimal concentration and the application way of Si. Therefore, for better understanding of the effect of Si on crop developments under field conditions, more

Table 2 Putative roles of exogenous silicon in legume salt stress tolerance in relation to antioxidant defense system induction

Legume species	Substrate	Salt stress		Exogenous silicon			Antioxidant responses to salt stress	References
		Level	Duration (day)	Form	Application way	Level		
Acacia gerrardii	Sand: perlite: peat	200 mM	56	K_2SiO_3	Growth solution	2 mM	Increased AsA, SOD, POD, CAT, APX and GR	[122]
Glycine max	Hydroponic condition	100 mM	1	Not shown		2 mM	Decreased APX, CAT and GSH	[104]
Glycyrrhiza uralensis	Sand	50 mM	10, 20, 30	K_2SiO_3		1, 2, 4 or 6 mM	Increased SOD and POD	[123]
	Filter paper	50, 100 or 150 mM	10			1, 2, 4, 6 or 8 mM	Increased SOD	[38]
	Sandy loam	6 g Kg^{-1}	70, 110			0.1 g Kg^{-1}	Increased AsA, GSH, APX, CAT, GPX and POD.	[91]
	Filter paper	100 mM	10			1 mM	Increased AsA, GSH, APX, CAT, SOD and POD.	[87]
Medicago sativa	Hydroponic condition	120 mM	15				Increased APX, CAT and POD	[45]
	Soil	50, 100 or 200 mM	28	Na_2SiO_3		2 mM	Increased CAT, SOD and POD	[73]
Phaseolus vulgaris	Ion-free sand	150 mM	30	K_2SiO_3	Foliar spray	6 mM	Increased glutathione, APX, CAT, SOD, POX and GR.	[105]
Vigna radiata	Sand : vermicompost	50 or 100 mM	29	Na_2SiO_3	Growth solution	3 mM	Increased APX, CAT, GR and SOD	[43]

Abbreviations: AsA, ascorbic acid; APX, ascorbate peroxidase; CAT, catalase; GR, glutathione reductase; GSH, glutathione; SOD, superoxyde dismutase; POD, peroxidase

studies using different Si forms and at varied doses are recommended.

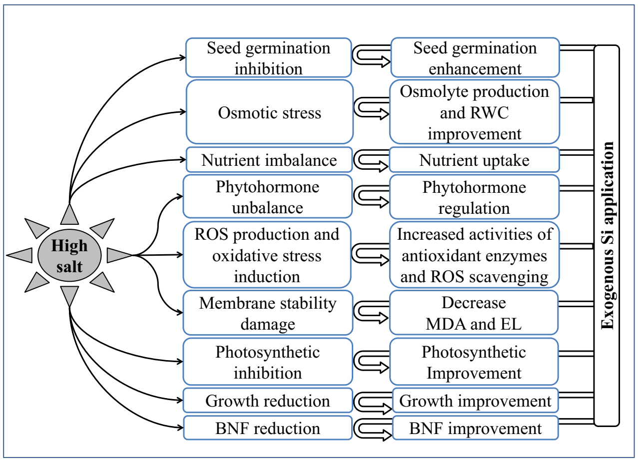

Fig. 5 Summary of the main effect of exogenous silicon (Si) application on legume salt tolerance. Abbreviations: Si, silicon; RWC, relative water content; ROS, reactive oxygen species; MDA, Malonyldialdehyde; EL, electrolyte leakages; BNF, biological nitrogen fixation

15 Conclusions

Legumes are important crop and they provide important nutrient source for human food and animal feed. They also fix atmospheric N with rhizobia, which allows them to ensure their N nutrition without any chemical fertilizers. However, legumes and their symbioses are very sensitive to abiotic stress, with a particular high sensitivity to salt stress. As salt stress causes both osmotic stress and ionic toxicity, it represents one of the major threats to legumes and its effect is observed at the different growth stages. Several works reported that exogenous Si was beneficial in improving plant salt-stress tolerance. Based on recent knowledge, Si showed a positive effect on legume seed germination, plant growth, development and productivity under salt stress (Fig. 5). Exogenous Si has also been confirmed to mediate BNF under diverse abiotic stress including salt stress. This is mediated by the positive effect of Si on nodule formation and size, leghemoglobin content and nitrogenase activity. Exogenous Si has also positive effects inside the nodules by increasing bacteroids and symbiosome number. Thus, it is clear from this review that Si has beneficial impact on legumes and its application under salt stress is recommended as a sustainable way for increasing growth, development, BNF and productivity of legumes.

16 Future Perspectives

Studies showed that Si uptake is an important factor for Si-induced plant tolerance to biotic and abiotic stresses [25, 26, 33, 36]. It is well documented that Si-uptake is related to the presence of some specific transporter called Lsi which ensure its transport from the soil solution into the plant cells [36]. Likewise, some plant family such as legumes has been considered as Si rejective, because the majority of the species belonging to this family does not have Lsi transporter [29]. However, although this plant family was considered as Si-rejective, Si application showed intriguing beneficial effects on plant growth of several legume species [42, 43, 74]. Furthermore, in some species like *G. max*, Si-induced salt stress tolerance was reported to be related to the presence of some specific Si-transported encoded by two genes, $GmNIP_{2-1}$ and $GmNIP_{2-2}$, which make this plant species a Si accumulator [63]. In addition, *M. truncatula* and *P. vulgaris* have been reported to have genes encoding for Lsi1 and Lsi2. *M. truncatula* was considered as mild Si accumulator [61]. Therefore, more studies on other legume species are required to identify new Si transporters and to better understand and clarify the ability of legumes to absorb Si.

Na^+ rejection from the cytosol or its compartmentalization into vacuole has been documented in several reports to be one of the most important strategies to overcome salt stress in plant [89]. Na^+/H^+ antiporters encoded by *SOS1* gene in the plasma membrane or by *NHX1* in the tonoplaste have been reported to have a crucial role in maintaining Na^+ homeostasis under salt conditions [36, 119]. Exogenous Si reduces Na^+ content in salt-stressed maize and this effect has been reported to be related to the ability of Si to upregulate the *SOS1* and *NHX1* gene expression [118]. Increasing K^+ content in plant under osmotic stress will help plants to maintain osmotic and cellular homeostasis [36, 133]. Its transport in plants was reported to be mediated by a high-affinity K^+ transporter (HKT) [134, 135]. In legumes, several studies have shown that Si reduced Na^+ and increased K^+ content [41, 117]. However, to date, no one has investigated the effect of Si on *SOS1*, *NHX1* and *HKT* gene expression in salt-stressed legumes. Therefore, it would be interesting to study how exogenous Si could induce salt tolerance in legumes through *SOS1*, *NHX* and *HKT* gene expression.

In agro-ecosystem, BNF through specific activity of nitrogenase represents one of the most important interests of legumes-rhizobia symbiosis [14, 17]. Some reports indicated that Si improves symbiosis establishment under salt stress [108]. However, to our knowledge, the effect of Si on nitrogenase activity under salt stress has not been studied yet. To better understand mechanisms by which exogenous Si improves BNF, the effect of Si on nitrogenase activity and on its gene expression particularly under salt stress will be important to be focused.

Maintaining water relationship in plant under osmotic stress is an important prospect for salt tolerance. Aquaporins, group of water channels, are known to mediate plant water uptake, and a positive correlation between aquaporins gene expression and tolerance to salt stress was observed in some plant species such as *Eutrema salsugineum* [136]. In some plant species like sorghum and cucumber, Si was reported to enhance water uptake under salt stress by upregulating aquaporins gene expression [85, 137]. However its effect on legume aquaporin related-gene expression is still poorly understood. Therefore, it would be interesting to investigate the effect of Si application on legume aquaporins gene expression particularly under salt stress.

Proline is known to play an important role in plant tolerance to diverse abiotic stress [93, 138, 139]. According to Szabados and Savouré [140], proline helps plant to maintain osmotic homeostasis, represent a ROS scavenger and N source. Studies reported in this review showed that the effect of Si on proline is species-dependent manner. Therefore, detail studies on the effect of exogenous Si on the expression of proline metabolism related-genes; *pyroline-5-carboxylase synthase* (*P5CS*), *Ornithine-δ-aminotransferase* (*OAT*) and *Proline dehydrogenase* (*PDH*); in legumes particularly under salt stress are needed to better understanding the effect of Si on proline metabolism.

Besides proline, the accumulation of glycine betaine and polyamines in legumes is a widespread response to salt stress [89, 141, 142]. Previous investigations showed that Si could alleviate salt stress in legumes through glycine betaine accumulation [43]. Furthermore, in *C. sativus*, Si-treatment increased salt tolerance highlighted by high polyamines content [143]. However, the specific mechanisms linking Si treatment with glycine betaine and polyamines accumulation in legumes under salt stress are not well understood. Therefore, further investigations are required particularly at the molecular level for a deeper understanding of the connection between Si treatment and glycine betaine and polyamines accumulation under salt stress.

Author Contributions Conceptualization, A.E.M. Writing-review and editing, A.E.M., N.L. and A.O. Comment on the content of the review and text revision, M.F., A.S. and M.M. Supervision, M.F. and A.S. Funding acquisition, M.F. and A.S. All authors contributed to the article and approved the submitted version.

Funding This work was supported by the Hubert Curien Maghreb Partnership - PHC Maghreb, No.19MAG41- governed by the agreement signed between the French Ministry of Europe and Foreign Affairs and the Algerian, Moroccan and Tunisian Ministries of Higher Education and Scientific Research.

Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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