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Salt stress tolerance mechanisms and potential applications of legumes for sustainable reclamation of salt-degraded soils

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Abstract

Soil salinity is considered one of the most detrimental environmental problems affecting the productivity of many agricultural crops, with negative effects on seed germination, plant vigour, and crop yields. To mitigate these negative effects, it is necessary to restrategize and identify viable options that are environmentally and economically applicable for sustainable agriculture. This review summarizes and evaluates soil reclamation strategies that have been employed and those that could potentially be used, concentrating on the use of legume crops. Apart from the fact that legumes have many nutritional benefits as foods, they are also an attractive option to refertilize degraded and nitrogen-deficient soils. Thus, the potential use of grain, grass, shrubby, and tree legumes to restore degraded soils requires evaluation. In this paper, we discuss and evaluate why legumes should be considered and used for the reclamation of degraded soils, with a particular focus on salt-degraded soils. Globally relevant case-studies that demonstrate how legumes could be used to reclaim salt-degraded soils are highlighted.

KEYWORDS

agricultural sustainability, increasing soil salinity, legumes, nutrient, reclamation, salt-degraded soil

1 | INTRODUCTION

Soil is a dynamic living resource with a complex mix of organic and inorganic materials and is important for agricultural productivity and human activities (Food and Agriculture Organization [FAO], 2015, www.fao.org). However, one-third of the world's agricultural soils are affected by soil degradation (Novara, Keesstra, Cerdà, Pereira, & Gristina, 2016; Prosdocimi et al., 2016), and increasing soil salinity is the major cause of soil degradation in many parts of the world (Abdelrahman, Burritt, & Tran, 2017; Abdelrahman, Jogaiah, Burritt, & Tran, 2018; Machado & Serralheiro, 2017; Wang, Tang, Wang, & Shao, 2015). Therefore, understanding the factors contributing to soil degradation, especially salinity, is essential in order to overcome this problem. Soil salinization can be caused by several environmental factors, including naturally occurring weathering of primary minerals, deposition of sea salt carried by winds, and inundation of coastal land by seawater (Mekonnen, Keesstra, Stroosnijder, Baartman, & Maroulis, 2015; FAO & Intergovernmental Technical Panel on Soils [ITPS], 2015). Soil salinization can also be caused by anthropogenic activities, including inappropriate fertilizer applications (Keesstra Geissen, Mosse, Piiranen, Scudiero, Leistra, & van Schaik, 2012; Tetteh, 2015), excessive irrigation with salt-containing water, and inadequate drainage systems (FAO & ITPS, 2015), unsustainable soil

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management practices such as overgrazing (Angassa, 2012; Hu, Liu, Yin, & Song, 2016; Mekuria & Aynekulu, 2013), deforestation, monocropping, up- and down-slope ploughing, and urbanization (FAO, 2015). In addition, rising sea levels due to global warming and the inundation of coastal areas due to natural disasters, such as tsunamis, can increase the salinity of coastal soils (Bhuiyan, Raman, & Hodgkins, 2017). For example, large areas along the coast in northeast Japan were confounded by a strong tsunami in 2011. The effect of salt water damage to agricultural soils was so severe that agricultural crops could not be grown in large stretches of the tsunami-flooded farmlands, even two years after the catastrophe (Roy, Sasada, & Kohno, 2014).

Increasing soil salinity is a global problem (Table 1), affecting approximately 20% of the irrigated agricultural land (about 60 million hectares [Mha]) worldwide (FAO & ITPS, 2015), and this could increase to 50% by 2050 due to global climatic changes (Abdelrahman et al., 2018; Bartels & Sunkar, 2005; Machado & Serralheiro, 2017). The FAO has reported that increasing soil salinity may take approximately 0.3 to 1.5 Mha of agricultural land out of production each year and reduce the yield potential of about 20 to 46 Mha (FAO & ITPS, 2015). In addition, if soil salinity is not managed and rises above certain salinity thresholds, crops cannot be grown (FAO, 2017). Currently, no accurate global statistics exist on the extent of salt-contaminated soils; and so, this information is required urgently. In 1990, the annual cost of land degradation by salinity was US$264 per hectare, which increased to US$441 per hectare in the year 2013 (Qadir et al., 2014; UNU-INWEH, 2014). Based on high-resolution satellite data and predictive modeling for crop plants, salinization has affected the yield of many agricultural crops in various areas in the United States, for example, the central California region is estimated to be losing approximately US$3.7 billion annually in agricultural revenue (Dove, 2017). On a global scale, the world loses an area larger than Manhattan (~5910 ha) in each week due to salt degradation, resulting in US$27 billion loss in crop value per year (Gies, 2017). If solutions are not found, this cost will continue to increase and this may pose serious threats to global crop production. In addition, it has been established that the effects of salinization on agricultural production directly influence the living conditions of farmers, the balance of natural ecosystems and the quality of natural resources, and the economies of many countries (http://www.fao.org/soils-portal).

TABLE 1 Estimates of the global distribution of land impacted by soil salinity provided by FAO (2015)

Regions	Extent of salinization (million hectares, Mha)
Africa	122.9
Asia	193.8
Australia	17.6
Europe	6.7
Middle East	91.5
North America	6.2
Central and South America	71.5

2 | THE IMPACTS OF SOIL SALINITY ON CROP PLANTS

Soil salinity inhibits the normal growth and development of most crop plants, and causes significant yields losses globally (Cao, Li, Liu, Kong, & Tran, 2018; Mantri, Patade, Renna, Ford, & Pang, 2012). The physiological impact of soil salinity on plants depends upon the compositions and concentrations of dissolved salts, as well as on the plant species of interest and the growth stage of the crop (Butcher, Wick, DeSutter, Chatterjee, & Harmon, 2016). For instance, saline soils contain excess soluble salts that are classified according to their electrical conductivity (EC) of the saturation soil extract in deciSiemen meter^{-1} (dS m^{-1}) into nonsaline (EC < 2 dS m^{-1}), slightly saline (EC = 2–4 dS m^{-1}), moderately saline (EC = 4–8 dS m^{-1}), and strongly saline (EC > 16 dS m^{-1}; Nackley & Kim, 2015). Accordingly, plant species are also classified into different groups depending on how they tolerate salt-affected soils. For example, glycophytes that represent the majority of crop plants tolerating only low salt content in soils (EC < 4 dS m^{-1}), whereas halophyte plants can complete their life cycles in high saline soils (EC > 4 dS m^{-1}; Nackley & Kim, 2015). Sodic soil is also a major problem for crop production. A sodic soil is a nonsaline soil (EC < 4 dS m^{-1}) that contains a large amount of exchangeable Na$^+$ (sodium adsorption ratio > 13) attached to clay particles, causing soil structure to slump and collapse rather than sticking together when contacting with water (Chi, Zhao, Sun, & Wang, 2012). The dispersed clay particles then block soil pores, and soil surface forms a dense impermeable surface layer that severely restricts water movement into the root zone and lowers oxygen content in rhizosphere (Chi et al., 2012). Saline–sodic soils possess properties of both sodic and saline characteristics including EC > 4 dS m^{-1}, sodium adsorption ratio > 13, and pH < 8.5 (Chi et al., 2012), whereas alkaline soils are mostly clay soils with a pH > 9 and a poor soil structure and infiltration capacity (Santini, Fey, & Smirk, 2013). Alkaline soils are not necessarily saline as the total amount of soluble salts in the soil is not excessive (EC < 4–8 dS m^{-1}), and the soils are mostly associated with the presence of Na_2CO_3 either as a result of irrigation or natural mineralization (Santini et al., 2013). Legumes tend to acidify soils to a greater extent in comparison with other species, which make it suitable for alkaline soil conditions to reduce the soil pH (Ferguson, Lin, & Gresshoff, 2013). Forage legumes are also effective in decreasing soil surface crusts due to their deep and large root system, which will improve the internal soil drainage and increase the soil-nitrogen (soil-N) content (Swanepoel & Tshuma, 2017). For instance, *Medicago sativa* is very tolerant to salt stress (up to 400 mM NaCl) and can be suitable for restoration of salt-degraded soils (Munns & Tester, 2008).

Many crop plants are classified as salt-sensitive, and their growth can be severely affected by saline conditions. Maize (*Zea mays*) is one of the major crops grown worldwide, and so it is vital to understand the impacts of salinization on the growth and development of maize to help reduce losses due to salinization. Maize is considered to be a more salt-sensitive crop compared with soybean (*Glycine max*) that is considered to be a moderately salt-susceptible crop (Butcher et al., 2016; Cao et al., 2018; Katerjia, van Hoorn, Hamdy, & Mastrorilli, 2000). However, high soil salinity can inhibit developmental process in soybean plants throughout their life cycles, from germination and vegetative growth to nodule formation and seed production (Phang, Shao, & Lam, 2008). Several other major crops also show reduced performance on saline soils including rice (*Oryza sativa*), which is sensitive from vegetative to reproductive stages (Ghosh, Ali, & Saikat, 2016; Hariadi, Nurhayati, Soeparjono, & Arif, 2015), and wheat (*Triticum aestivum*; Alom, Hasan, Islam, & Wang, 2016; Sharma, 2015). Salinity also has an adverse effect on shoot biomass, pod set, and pod filling in chickpea (*Cicer arietinum*), causing reduced yields (Atieno et al., 2017; Flowers et al., 2010). Many vegetable crops are also susceptible to salinity stress, with the threshold (EC_t) of the majority of these crops being between 1 and 2.5 dS m^{-1} in saturated soil extracts, but variability exists among different crops, such as sweet pepper (*Capsicum annuum*), tomato (*Solanum lycopersicum*), and cucumber (*Cucumis sativus*; Machado & Serralheiro, 2017). As saline soil has the potential to reduce yields of many essential food crops, efforts must be channeled toward the utilization of sustainable means to reclaim salt-contaminated soils in addition to preventing further contamination.

3 | CONVENTIONAL METHODS FOR THE REMEDIATION OF SALINE SOILS

As soil salinization can be a continuous process, its remediation is often labor-intensive and costly (Hasanuzzaman et al., 2014). The first step in managing salt-contaminated soils is to identify the cause of contamination. Identifying the cause of soil salinization can be difficult, especially if multiple factors are involved. After determining the cause, the second step is to determine a management plan (McCauley & Jones, 2005). Choosing how to manage increasing soil salinity and which mitigation/reclamation techniques to employ depend on a number of factors, including cropping system(s), the availability of fresh water, and cost (Machado & Serralheiro, 2017; McCauley & Jones, 2005). Reclamation techniques can include physical, chemical, hydro-technical, and electro reclamation (Ahmed & Qamar, 2004; Larney & Angers, 2012; Legwaila, Lange, & Cripps, 2015; Zia-ur-Rehman et al., 2016), but many techniques are considered inappropriate, due to their unfriendly, unsustainable, and uneconomical status.

Briefly, physical techniques, such as deep ploughing, subsoiling, horizon mixing, sanding, profile inversion, and channeling irrigation practices, can improve the permeability of the soil, which has been known as a limiting factor during the reclamation of saline soils (Ahmed & Qamar, 2004; Zia-ur-Rehman et al., 2016). However, this approach is costly and can be limited by the availability of fresh water (Shrivastava & Kumar, 2015). Chemical techniques include the applications of gypsum, sulfur, sulfuric acid, or hydrochloric acid (Ahmed & Qamar, 2004; Zia-ur-Rehman et al., 2016). Gypsum application has been considered an economical method for the remediation of saline soils (Schultz, Chatterjee, DeSutter, & Franzen, 2017; Zia-ur-Rehman et al., 2016). Gypsum possesses a quite low relative solubility (0.2%) in water, and this can extend the reclamation process (Carter & Pearen, 1989). Efficient mixing of the soil with gypsum and rapid removal of sodium from the soil solution by proper irrigation will fasten the exchange process (Frenkel, Gerstl, & Alperovitch, 1989). However, if the soil is condensed and has low drainage capacity, sodium ions are not readily displaced by gypsum calcium ions and leaching of sodium ions by irrigation water or rainfall can be largely ineffective, and the salinity of the soil water can actually increase (Ilyas, Qureshi, & Qadir, 1997; Zia-ur-Rehman et al., 2016). It should also be noted that chemical applications can inhibit microbial respiration and enzymatic activities (Norton & Strom, 2012), and this could affect the reclamation processes as microbes play important roles in healthy soils (Ali, Abdelrahman, Radwan, El-Zayat, & El-Sayed, 2017). Although the hydro-technical technique is ineffective without gypsum application, the electro-reclamation technique remediates saline soils through electrodialysis (Zia-ur-Rehman et al., 2016). Field investigations and laboratory analyses have shown that treatments with electric currents may facilitate the reclamation of saline soils (Abdel-Fattah, 2014), although it cannot be used to completely replace the more conventional procedures used for the reclamation of saline soils (Zia-ur-Rehman et al., 2016). In addition, a major problem associated with the electro-reclamation technique is the presence of insoluble compounds, such as $CaSO_4$, in soils that have the potential to decrease the responsiveness of soils to electro-reclamation (Nasim, Oh, & Chai, 2012; Zia-ur-Rehman et al., 2016).

In addition to chemical and physical methods, phytoremediation was recently introduced as a potential cost-effective biological technique to reduce salinity by removing salt ions from the soil, thereby maintaining agricultural sustainability (Hasanuzzaman et al., 2014). For example, de Souza et al., (2012) investigated the effects of the halophyte plant *Atriplex nummularia* on the chemical properties of saline–sodic soil and revealed a significant reduction in the soil salinity after cultivation of *A. nummularia* plants without the adverse effects on their growth and biomass production. The high yields of *A. nummularia* under high salinity indicate the potential application of this halophyte for restoration of salt-affected soils. In another study, phytoremediation of saline soils was examined using seven different plant species, including wheat (*T. aestivum*), Indian mustard (*Brassica juncea*), field mustard (*Brassica campestris*), Egyptian clover (*Trifolium alexandrianum*), sunflower (*Helianthus annuus*), millet (*Sorghum bicolor*), and spinach (*Spinacea oleracea*; Bareen & Tahira, 2010). Of these species, spinach followed by *Brassica* spp. exhibited the highest accumulation of Na^+, whereas the greatest dry weights were detected in millet followed by sunflower and spinach (Bareen & Tahira, 2010). These results suggest that spinach followed by *Brassica* spp. could be the best candidates for phytoremediation.

Evolving efficient, low cost, easily adaptable techniques to reduce the impacts of soil salinization remains a major challenge (Shrivastava & Kumar, 2014). The key question is how we can reclaim already degraded soils in a way that will be economically beneficial, environmentally safe and sustainable? Legumes are already recognized for their ability to improve degraded soils, due to their atmospheric nitrogen (N_2) fixation ability that can lead to improved soil quality, strengthened soil biochemical cycling, and increased soil microbial activities (Abdelrahman et al., 2018; Maikhuri, Dangwal, Negi, & Rawat, 2016; Pérez-Fernández, Calvo-Magro, & Valentine, 2016). In addition, legumes also have potential as a sustainable means to help reclaim salt-contaminated soils, which we critically evaluate in the next sections.

4 | WHY SHOULD LEGUMES BE CONSIDERED AND SELECTED FOR RECLAIMING SALT-CONTAMINATED SOILS?

The advantage that N-fixing legumes have over N-non-fixing plants for reclaiming saline soils is that they not only have the potential to remove toxic ions but also to increase soil-N levels. For example, *Hedysarum carnosum*, a pastoral legume, was able to increase Na^+ accumulation in the roots and maintain high symbiotic N_2 fixation (SNF) efficiency and subsequent soil-N content under high salinity (100 mM NaCl), suggesting its potential utilization in the improvement of soil fertility under saline conditions (Kouas, Slatni, Ben Salah, & Abdelly, 2010). Also, tree legumes such as *Acacia nilotica* and *Leucaena leucophela* have been grown as fodder under saline conditions with slight reduction in SNF efficiency at 90 mM NaCl (Bruning & Rozema, 2013). These examples indicate that growing N-fixing legumes can be considered as an option for restoration of salt-degraded soil in comaprision with N-non-fixing plants. Recently, maize have been shown to be able to reclaim saline–sodic soils in China (Luo et al., 2018). On the other hand, soybean has been generally considered as more tolerant to saline soils than maize (Butcher et al., 2016; Katerjia et al., 2000); and thus, it would be worth testing its ability in restoring saline–sodic soils in the same areas, given it can also supply N to the soils. Indeed, legumes have long been recognized and valued as "natural soil fertilizers". They promote nutrient cycling, increase the incorporation of carbon into soils, restore soil nutrients, and minimize erosion and can therefore aid in the establishment of other plant species (Lange et al., 2015; de Moura et al., 2016). Although forage and grain legumes have been used in agricultural systems for many years, their potential to aid in reclaiming salt-degraded soils was only recently proposed (El Shaer & Al Dakheel, 2016). For example, tree legumes have been identified as the best alternative to overcome soil-N depletion associated with salt-degraded forest soils (Marcar, Ismail, Hossain, & Ahmad, 1999), with selection and planting of appropriate tree legumes as a viable means to reintroduce N into salt-degraded soils (Ogle, & John, 2010; Singh, Singh, Singh, & Cerdà, 2017).

Salt-tolerant legumes can be obtained through either conventional or molecular marker-assisted procedures that help to introduce new tolerance traits into elite lines of grain legumes for the sustainable restoration of salt-degraded soils (Foyer et al., 2016; Mishra, Panda, & Sahoo, 2014; Yasuta & Kokubun, 2014). With respect to selecting and breeding legume cultivars with the potential to be used for reclaiming saline soils, field phenotyping is becoming the method of choice (Campbell et al., 2015; Khan, Siddique, & Colmer, 2016; Roy et al., 2014; Tuberosa, 2012). For example, Vadez et al. (2015) utilized a high-throughput, three-dimensional scanning method to observe leaf development in relation to plant water use in peanut (*Arachis hypogaea*) and cowpea (*Vigna unguiculata*) plants to gain a better understanding of the physiological processes associated with salinity stress. Atieno et al. (2017) used a high-throughput, nondestructive, phenotyping platform to investigate 245 diverse accessions of chickpea to identify important agronomic traits for chickpea salt tolerance. Broad genetic variation for plant height, growth rate, leaf senescence, flowering period, shoot biomass, pod and seed numbers, and shoot Na^+ and K^+ levels under saline conditions and salinity tolerance traits were identified. Of note, the authors found that seed number was a major contributor to yield under saline conditions, and therefore an important trait when breeding chickpea cultivars for improved salt tolerance. The phenotypic data obtained from such field screening studies can be linked to genotypic data and used for genome-wide association mapping to identify loci that underlie salinity tolerance in chickpea (Atieno et al., 2017). Such an approach could also be explored for other legumes to develop better yielding salt-tolerant cultivars. Soybean has also been identified as a promising crop for reclamation of salt-degraded soils due to its salt-tolerant status (Cao et al., 2018). A number of genes, including those involved in ion compartmentalization, Na^+ exclusion, and anti-oxidative processes, as well as those encoding transcription factors and other regulatory proteins such as calmodulins and calcineurin B-like proteins, have been identified in soybean (Cao et al., 2018; Pi et al., 2016; Qi et al., 2014; Wong, Li, Yao, & Lam, 2013; Zhang et al., 2010; Zhou et al., 2014). Although field application of soybean for the reclamation of saline soils still remains a challenge (Cao et al., 2018), strong lines of evidence have shown that further research may uncover more salinity tolerance-associated genes in soybean, which will eventually pave the way for other leguminous crops to be used for the reclamation of salt-degraded soils.

5 | INSIGHT INTO MECHANISMS REGULATING SALT STRESS TOLERANCE IN LEGUMES AND SYMBIOTIC RHIZOBIA—SUITABLE MECHANISISMS FOR RESTORATION OF SALT-DEGRADED SOILS

5.1 | Salt stress tolerance in symbiotic rhizobia

To maximize the potential of legumes for the reclamation of salt-degraded soils, they need to establish symbiotic relationship with rhizobia (Borges, Prin, Ducousso, Le Roux, & de Faria, 2016; Coba de la Peña & Pueyo, 2012). Thus, restoration of salt-degraded soils depends not only on salt-tolerant legumes alone (Bruning et al., 2015; Coba de la Peña & Pueyo, 2012; Zahran, 1999) but also on the survival of rhizobia under saline conditions (Coba de la Peña & Pueyo, 2012; Swaraj & Bishnoi, 1999; Ventorino et al., 2012; Zahran, 1999). Rhizobia subjected to salt stress readjust, adapt, and may undergo morphological alterations, including changes in cell morphology and size, or modifications in the patterns of extracellular polysaccharides and lipopolysaccharides (Ventorino et al., 2012). Pereira, Lima, and Figueira (2008) reported that salinity tolerance of rhizobia could be due to plasmid-mediated tolerance, as salt tolerance can be rapidly transferred from tolerant bacteria to sensitive ones through plasmids. Thus, extrachromosomal genetic elements, and changes in gene expression (López-Gómez, Palma, & Lluch, 2013), can contribute to adaptive mechanisms and the survival of rhizobia in saline soils. These suggestions are supported by the findings of Andrew and Andrew (2017) who showed that lateral transfer of symbiosis-specific genes within rhizobia genera is an important mechanism allowing legumes to form a symbiosis with rhizobia adapted to particular soils.

5.2 | Salt stress tolerance in legumes

Salt stress tolerance in legumes is associated with changes in several molecular, biochemical, and physiological processes, including sequestering of Na^+, induction of antioxidative stress responses, and accumulation of osmoprotectants (Bargaz et al., 2015; Zhang et al., 2017). A recent study was performed using transcriptome analysis to investigate the molecular response of 12 *M. sativa* genotypes (G01–G12) under salt stress conditions (Sandhu, Cornacchione, Ferreira, & Suarez, 2017). Of these genotypes, G03 displayed up-regulation of the *salt overly sensitive* (*SOS1*, *SOS2*, and *SOS3*) genes involved in Na^+ efflux from roots to soil, and this G03 genotype showed a limited increase in shoot-Na^+ content and the highest growth biomass (Sandhu et al., 2017). On the other hand, G12 genotype exhibited the highest accumulation of Na^+ with almost 25% reduction in the number of shoots and plant height. The growth capability of G12 under salt stress was attributed to the up-regulation in the *Na^+/H^+ antiporter* (*NHX1* and *NXH2*) and *high-affinity K^+ transporter1* (*HKT1*) genes involved in the partition of Na^+ into vacuoles to protect the cytosol from the Na^+ toxic effect, and to retrieving Na^+ from xylem into roots to keep the Na^+ content low in the shoots (Sandhu et al., 2017). The *SOS1* gene has been known to play a significant role in salt stress tolerance, and transgenic tobacco (*Nicotiania tabacum*) overexpressing the halophyte *Salicornia brachiata SbSOS1* gene exhibited high salt tolerance relative to wild type plants (Yadav, Shukla, Jha, Agarwal, & Jha, 2012). Transgenic tobacco plants exhibited reductions in levels of reactive oxygen species and electrolyte leakage in response to salt stress, which occurred due to the decrease in the cytosolic Na^+ content (Yadav et al., 2012). In addition, transgenic tobacco plants displayed a significant increase in seed germination, fresh and dry weights, relative water content, K^+/Na^+ ratio as well as proline and amino acid contents under high salinity in comparison with wild type plants (Yadav et al., 2012). These results expand the important role of *SOS1 in planta* and indicate that the *SOS1* gene could be used to improve salt tolerance of various crops. In another study, comparative ecophysiological analysis of salt stress tolerance in wild (*Glycine soja*) and cultivated soybean was carried out (Wu et al., 2014). Wild soybean was able to maintain higher relative water content, accumulate higher amount of osmolytes, including proline and glycine betaine, and increase K^+ influx and Na^+ efflux to keep higher K^+/Na^+ ratio (Wu et al., 2014). The obtained results indicated that the wild soybean has different tolerance mechanisms or different levels of same mechanism(s), which ensure its better salt tolerance as compared with cultivated soybean. Thus, wild soybean can be used as an eminent germplasm to enhance salt stress tolerance in soybean (Wu et al., 2014). The above examples provided an insight into mechanisms that enable various legumes to adapt to salt stress and, thus, can further be explored for the development and selection of salt-tolerant legumes for the restoration of salt-degraded soils. On a more general note, transcriptomic approaches are being complemented by proteomics, metabolomics, and functional genetic studies, and new genes and traits are being identified in legume cultivars and rhizobia that might be suitable for the reclamation of salinity-degraded soils (Andrew & Andrew, 2017; Coba de la Peña & Pueyo, 2012; Mishra et al., 2014; de Moura et al., 2016; Murray, Liu, Chen, & Miller, 2017). Also, identification of high-affinity K^+ transporters, which function to increase K^+ influx and K^+/Na^+ ratio and prevent the accumulation of toxic ions in the leaves, is a priority for many crop legumes, if they are to be grown on saline soils (Jez, Lee, & Sherp, 2016).

5.3 | Suitable salt tolerance mechanisms of legumes for restoration of salt-degraded soils

Generally, a sustainable salt tolerance mechanism, desirable for legumes as well as restoration of salt-contaminated soils, is the one that could enable the legume plants to uptake and store of salt ions (e.g., Na^+ and $Cl^−$), and legume-rhizobium symbiosis restores the soil nutrients (Figure 1). This is important as salt ions can be safely removed from the soil, and at the same time, soil nutrients can be restored. For example, López-Aguilar, Orduño-Cruz, Lucero-Arce, Murillo-Amador, & Troyo-Diéguez (2003) investigated the uptake and transport rate of Na^+ ions in cowpea, frijolillo (*Phaseolus jiliformis*), and tepary bean (*Phaseolus acutifolius*) grown under salt stress conditions and revealed a higher net Na^+ uptake in the salt-treated tepary bean roots than in salt-treated cowpea and frijolillo roots. However, the net Na^+ transport from roots to shoots was lower in salt-treated terpary bean in comparison with salt-treated cowpea and frijolillo. These results indicated that Na^+ was highly accumulated in the tepary bean roots rather than shoots, whereas an opposite trend was observed in cowpea and frijolillo plants (López-Aguilar et al., 2003). Plant height was generally reduced in the three legume species under salt stress conditions in comparison with control; however, the plant height of salt-treated tepary bean was greater than salt-treated cowpea and frijolillo plants. In addition, the dry weight of roots, leaves, and stems of salt-treated tepary bean was greater than that of

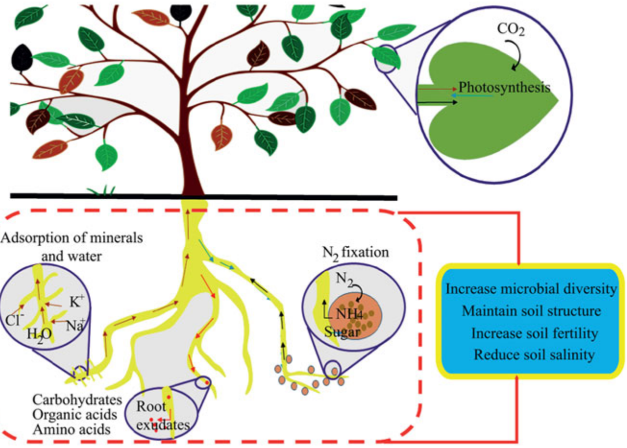

FIGURE 1 Diagram representing reclamation of salt-degraded soils using legumes. During reclamation, root exudates (carbohydrates, organic acids, and amino acids) interact and activate nitrogen (N_2)-fixing rhizobia present in root nodules. In addition, legumes increase ion (Na^+, $Cl^−$, and K^+) uptake from the soil into the roots and translocation from roots to foliar tissues. N_2 fixation, root exudates and increased ion uptake from salt-contaminated soils increase microbial diversity, maintain soil structure and fertility, and reduce soil salinity [Colour figure can be viewed at wileyonlinelibrary.com]

salt-treated cowpea and frijolillo plants. This result indicated that tepary bean exhibited salt tolerance mechanism through high uptake rate of Na$^+$ in the roots and low Na$^+$ mobility to the shoots. In another study, Bruning et al. (2015) examined the effect of high soil salinity on *Melilotus officinalis* and *M. sativa* growth and their SNF efficiency. The biomass of *M. officinalis* and *M. sativa* was more significantly reduced under higher level (12–20 dS m^{-1}) than lower level (1.7–8 dS m^{-1}) of salt stress. However, both species maintained their plant-N content, probably through maintenance of their normal SNF, under a wide range of salt stress, which was only reduced by high salinity levels ≥20 dS m^{-1} (Bruning et al., 2015). Similarly, data on SNF and growth of *Sesbania sesban*, *Acacia dealbata*, *Sesbania rostrate*, and *Casuarina equisetifolia* under different salt stress levels showed a significant reduction in SNF and growth of all species, with the exception of *C. equisetifolia* that maintained the wild-type level of SNF efficiency and growth biomass even under high soil salinity (200 mM NaCl; Bruning et al., 2015; Mahmood, Athar, Qadri, & Mahmood, 2008). The above examples demonstrated the high capacity of some legume species to uptake salt ions, while maintaining efficient SNF under salinity, which is an important mechanism for the restoration of saline soils (Figure 1). In addition to the significant contribution of legumes to the uptake of salt ions, growing legumes improves soil chemical, physical, and biological properties; however, the extents of these soil improvements depend mainly on the type of legumes used. For example, forage legumes are much effective in improving soil quality than annual grain legumes due to their longer growth period, deeper and larger root system, and greater SNF capacity, enabling them to produce large quantities of organic matter and N in the soils (Bardgett, Mamer, & De Vries, 2014; Dane, Laugale, Lepse, & Siliņa, 2017). The deep and large root system of legumes opens the ways that help increase soil porosity and promote air movement and water drainage even in deeper layers of soils (Bardgett et al., 2014; Dane et al., 2017). In addition, legume root exudates, including carbohydrates and proteins, can increase soil aggregation and reduce soil erosion and crusts (Bardgett et al., 2014; Van Eerd et al., 2013).

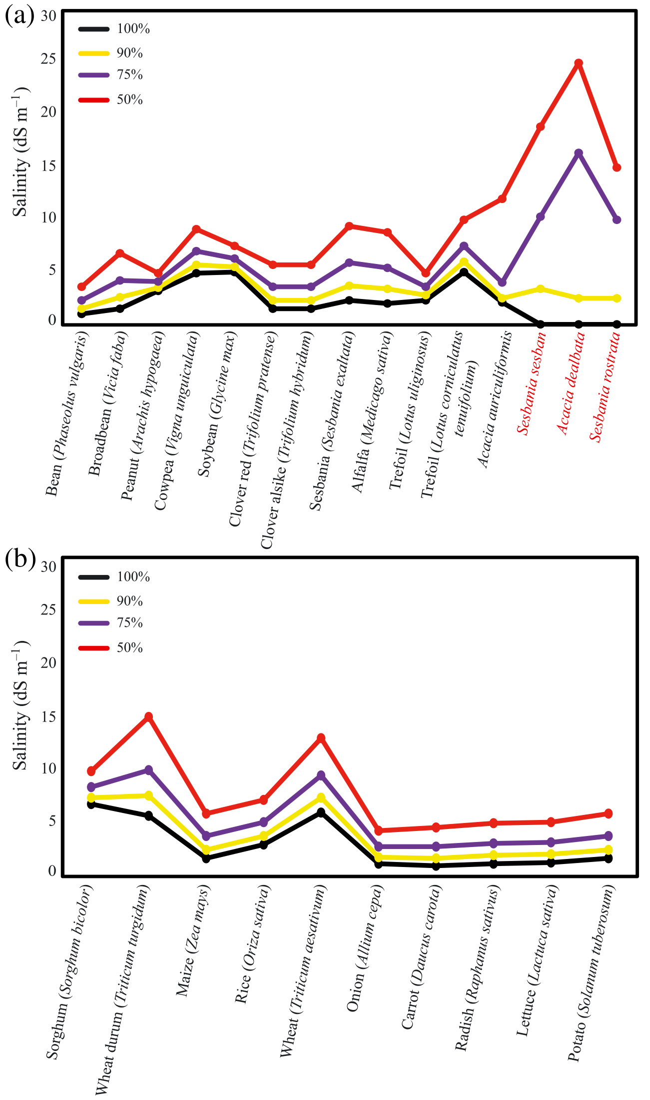

FIGURE 2 Yield potential (50%, 75%, 90%, and 100%) of different legume species (a), and cereal and vegetable crops (b) at various salinity levels (deciSiemen [dS m^{-1}]) according to www.fao.org [Colour figure can be viewed at wileyonlinelibrary.com]

A few legumes, including strawberry clover 'Salina' and *Melilotus siculus* 'Messina', have been commercially released for cultivations on high saline soils (Ogle & John, 2010), indicating that some other legume species could also be selected as promising candidates for reclamation of salt-degraded soils. Figure 2 provides a comparative analysis of yield potential of different legumes, cereals, and vegetables at various soil salt concentrations (www.fao.org). The comparative analysis showed higher salt tolerance levels and yield potential of *A. dealbata*, *S. sesban*, *S. rostrata* legume trees under high salt concentrations >10–25 dS m^{-1} relative to cereal and vegetable crops (Figure 2). Thus, these legume species can be used for the reclamation of salt-degraded soils, by using them as a tree-fence-plot. Additionally, a list of potential registered legume cultivars for different levels of salinity, pH, and soil types according to the Australian soil salinity test are summarized in Table 2. For example, strawberry clover 'Salina' and *M. siculus* 'Messina' are commercially available for seeding in high-saline soils and, thus, can be used for the restoration of salt-degraded soils (Ogle & John, 2010). After selecting a proper legume variety for salt land, legume seeds should be sown soon after rains have leached salt from the soil surface (www.agric.wa.gov.au/soil-salinity/pasture-legumes-and-grasses-saline-land?nopaging=1). Legume seeds should be pre-inoculated with a *Rhizobium* strain suitable for the legume species prior to sowing. This is particularly essential in salt land, as rhizobial levels are likely very low. In addition, intercropping system is also an effective way to improve soil properties and yield under high saline conditions. A case-study of cereal-legume intercropping system in a moderately degraded alfisol in Pakistan, which was characterized with high aluminum- and iron-bearing minerals in the surface layers and relatively high calcium and sodium ions in the lower layers, was recently reported (Ahmed, Khan, Shah, & Khan, 2017). The authors reported that cereal-legume rotation system (maize–lentil–maize–lentil cycle; from 2006 to 2007) all year round was the best management practice for sustained production on this type of degraded alfisol (Ahmed et al., 2017). However, assessment of the rotational disadvantages/advantages based on multispecies rotation, planting method, and duration is important to formulate adequate conclusions. For example, Mahallati, Koocheki, Mondani, Feizi, and Amirmoradi (2015) suggested

TABLE 2 List of registered legume cultivars for different categories of salinity range and their relationship to soil texture according to the Australian soil salinity classification test (www.agric.wa.gov.au/soil-salinity/pasture-legumes-and-grasses-saline-land?nopaging=1)

Salinity range (dS m^{-1})	pH	Soil type	Registered name	Scientific name
Moderate (4–8)	5.8–9.0	Loam–clay	Barrel medic	*Medicago truncatula*
Moderate to high (4–8 to 8–16)	5.2–8.5	Sandy loam–clay loam	Burr medic	*Medicago polymorpha*
Moderate (4–8)	5.8–9.0	Loam–clay	Snail medic	*Medicago scutellata*
Moderate to severe (4–8 to 16–32)	5.5–9.0	Sandy loam–clay	Messina	*Melilotus siculus*
Moderate to high (4–8 to 8–16)	4.5–8.0	Loam–clay	Bokhara clover	*Melilotus albus*
Low–moderate (2–4 to 4–8)	4.5–8.0	Sandy loam–loam	Balansa clover	*Trifolium michelianum*
Low–moderate (2–4 to 4–8)	5.6–9.0	Sandy loam–clay	Strawberry clover	*Trifolium fragiferum*

that strip width of two rows of maize alternated with three rows of bean strip intercropping was superior compared with monoculture method. In salt-degraded areas, soil salinity levels can differ widely even within a few meters, therefore, it is better to evaluate the field for degree and extent of the salinity problem prior to making decision for selecting appropriate approach for soil restoration. Combining a number of salt-tolerant legumes might be the best approach to deal with a field with high variation of salinity level.

6 | GLOBAL ATTENTION ON LEGUMES AS A SUSTAINABLE TOOL FOR RECLAMATION OF SALINE SOILS

Legumes have become an important global bioresource not only for N_2 fixation (Lange et al., 2015; Maikhuri et al., 2016) but also for reclamation of saline soils (Bruning et al., 2015). A typical example is *M. siculus* that originated from marshy, saline areas of the Mediterranean basin, East Asia, and Iberian Peninsula (Marañón, Garcia, & Troncoso, 1989). Nichols et al. (2010) conducted field experiments in different regions of southern Australia and found that out of 33 self-regenerating annual legumes, *M. siculus* (Turra) Vitman ex B.D. Jacks was the only promising pasture legume for saline waterlogged (ECe levels in summer >8 dS m^{-1} in the top 0–10 cm) soils. Bhuiyan, Maynard, Raman, Hodgkins, Mitchell, & Nicol (2016) also demonstrated the outstanding performance of *M. siculus*, in comparison with *Thinopyrum ponticum* (Poaceae) and *Tecticornia pergranulata* (Amaranthaceae), in a glasshouse-pot trial using salt concentrations of 0.0, 2.5, and 5.0 dS m^{-1}. Thus, *M. siculus* appears to be the candidate-of-choice for the restoration of saline areas in central western New South Wales of Australia.

Although in Australia, *M. siculus* is more salt-tolerant than all other current pasture legumes (Countryman, 2017), in other parts of the world beach pea (*Vigna marina*), found on tropical and subtropical beaches around the world (along the Atlantic and Indian Ocean coasts of Asia, Africa and Australian coasts, and islands in the Pacific Ocean and the Caribbean), also has the potential to be used for the reclamation of salt-affected areas (Buddenhagen, 2014). Another legume with reclamation potential is *Sulla carnosa*. Naturally nodulated *S. carnosa* plants of the saline biotope (sebkha d'El kelbia) were obtained from the fields in Tunisia, and their symbiotic-efficiency and feed production potentiality were investigated (Hajer, Hbib, & Abdelmajid, 2017). Both field and greenhouse studies were used to demonstrate that *S. carnosa* is a good candidate for saline agriculture due to its ability to grow, produce biomass, and fix N_2 under high soil salinity (about 150 mM NaCl). *S. carnosa* protects its photosynthetic and symbiotic N_2-fixing capacities by regulating Na^+ uptake and accumulating Na^+ in the roots. *S. carnosa* has the potential to allow the sustainable development of soils traditionally considered to be marginal for crop production and further studies are underway that aiming to explore the genotypic variability of populations of *S. carnosa* plants from different parts of Tunisia with respect to salinity tolerance (Hajer et al., 2017).

The growth of alfalfa *(M. sativa)* in saline regions of the Egytian Sinai Desert has also been achieved, with plants showing good salt tolerance, high biomass production and high nutrient values (El Shaer & Al Dakheel, 2016). Thus, alfalfa has the potential to make a positive contribution to agricultural production in regions with salt-degraded soils and hence to enhance the living standards of people living in these areas. In the United States, an extensive breeding program began in 2010 to evaluate and screen alfalfa plants for salt tolerance under field conditions (Hayward, 2015). The program included comparing plants selected for salt tolerance with new varieties and existing breeding lines and measuring the growth of plants irrigated with pure or salt water. Genotypes were identified that performed well in the fields in both the presence and absence of salt.

In Europe, several countries are also beginning to use legumes to both fix N_2 and to reduce soil salinity (Graves et al., 2015; Qadir et al., 2014). Field experiments conducted in the Netherlands investigated the efficiency of N_2 fixation by legumes at varying saline levels (Bruning et al., 2015). Based on their results, sweet clover (*M. officinalis*) fixed substantial amounts of N_2 at moderate soil salinities, with the fixed-N becoming available in the soil (and thus available to crops) when legumes senesced and decomposed. Bruning et al. (2015) concluded that sweet clover has a promising future for the reclamation of saline soils in temperate regions. Research in India and other Asian countries has also shown the usefulness of legumes for the reclamation of salt-degraded soils (Li, Yang, Redden, He, & Zong, 2016; Mishra et al., 2014; Wong et al., 2013). Lalita & Bhardway (1981) confirmed that despite being grown on moderately saline soils, the growth, nodulation, and N_2 fixation of several Indian legume crops were good; especially, dhaincha (*Sesbania aculeate*) and Indian clover (*Trifolium albopurpureum*) were both outstanding. At high soil salinity, exchangeable sodium percentage of 70, only dhaincha and Indian clover could grow and nodulate (Lalita, B. & Bhardway, 1981).

7 | CONCLUSIONS

The reductions in the quality and quantity of arable land and water coupled with food security concern due to the anticipated increase in population growth have put productivity enhancement of salt-degraded lands on the world agenda. Simple projections suggested that the global annual cost of land degradation by salinity could be US$ 27.3 billion due to the reduction in crop productivity. In addition, other cost impacts such as infrastructure deterioration, employment losses, and associated environmental costs cannot be also neglected; and thus, the actual loss by salt-induced land degradation is higher than expected. Therefore, efforts to deal with this land degradation problem should be beyond the typical farm salinity management and include (a) establishment of salt-tolerant tree and crop species, (b) improvement of irrigation and drainage network, (c) undertaking water and soil quality tests at different times to select a suitable approach for soil treatment, and (d) capacity building for local farmers to follow up the recommended salinity management approaches.

Soil salinity is a global problem; however, legumes have a recognized ability to restore nutrients to salt-degraded soils and the potential to remove toxic ions if properly utilized, maintained, and sustained. Prior to restoration of salt-degraded soils, all environmental, biological, and technological protocols for remediation should be appropriately assessed. Field trials should be used to complement both laboratory and glasshouse experiments for the selection of salt-tolerant legumes and symbiotic rhizobial partners suitable for the restoration of salt-degraded soils. The rapid progress in genome sequencing technologies has enabled the identification of valuable genes associated with salt tolerance in legumes, and these could be used through genetic engineering to enhance the adaptations of legumes in order to effectively reclaim salt-degraded soils.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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