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Review

Effects, tolerance mechanisms and management of salt stress in grain legumes

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A B S T R A C T

Salt stress is an ever-present threat to crop yields, especially in countries with irrigated agriculture. Efforts to improve salt tolerance in crop plants are vital for sustainable crop production on marginal lands to ensure future food supplies. Grain legumes are a fascinating group of plants due to their high grain protein contents and ability to fix biological nitrogen. However, the accumulation of excessive salts in soil and the use of saline groundwater are threatening legume production worldwide. Salt stress disturbs photosynthesis and hormonal regulation and causes nutritional imbalance, specific ion toxicity and osmotic effects in legumes to reduce grain yield and quality. Understanding the responses of grain legumes to salt stress and the associated tolerance mechanisms, as well as assessing management options, may help in the development of strategies to improve the performance of grain legumes under salt stress. In this manuscript, we discuss the effects, tolerance mechanisms and management of salt stress in grain legumes. The principal inferences of the review are: (i) salt stress reduces seed germination (by up to more than 50%) either by inhibiting water uptake and/or the toxic effect of ions in the embryo, (ii) salt stress reduces growth (by more than 70%), mineral uptake, and yield (by 12–100%) due to ion toxicity and reduced photosynthesis, (iii) apoplastic acidification is a good indicator of salt stress tolerance, (iv) tolerance to salt stress in grain legumes may develop through excretion and/or compartmentalization of toxic ions, increased antioxidant capacity, accumulation of compatible osmolytes, and/or hormonal regulation, (v) seed priming and nutrient management may improve salt tolerance in grain legumes, (vi) plant growth promoting rhizobacteria and arbuscular mycorrhizal fungi may help to improve salt tolerance due to better plant nutrient availability, and (vii) the integration of screening, innovative breeding, and the development of transgenics and crop management strategies may enhance salt tolerance and yield in grain legumes on salt-affected soils.

Contents

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1. Introduction

Salt-affected soils contain excessive soluble salts and exchangeable sodium on the surface or in the rhizosphere. Salt stress is one of the major constraints to profitable crop production as it affects >800 million (ha) of land around the world (FAO, 2008). Other than natural causes such as salty water on the coasts and contamination from parent rock and oceanic salts, erroneous cultivation practices have contributed to increasing salt concentrations in the rhizosphere (Rengasamy, 2010). Salinization of arable land is increasing worldwide, threatening the productivity of arable land under cultivation.

Salt stress involves osmotic stress, ionic imbalances, and secondary stresses such as nutritional imbalances and oxidative stress for glycophytes (Deinlein et al., 2014). Although Na^+ is the dominant ion causing toxicity under salt stress, some plant species are also sensitive to Cl^-, the major anion in salt-affected soils. High concentrations of salts disturb the osmotic balance resulting in 'physiological/secondary drought', which restricts plant water uptake (Farooq et al., 2015).

Grain legumes are a low-cost and nourishing food from the family *Fabaceae*. They are rich in dietary proteins (17–40%), complex carbohydrates, essential amino acids, vitamins, fiber, and minerals. Crop rotations that include legumes are an effective strategy for improving soil fertility and crop yields due to the biological nitrogen (N) fixation ability of legumes. The ability of legumes to fix N, from physiologically non-available molecular dinitrogen (N_2) to available forms, makes them unique in terms of providing an N skeleton to different life forms (Qureshi et al., 2010). Legumes occupy 12–15% of arable land worldwide to produce 27% of major crop production and provide 33% of dietary protein (Mishra et al., 2014). Being a rich source of protein, legumes are a dietary staple for millions of humans and animals.

Salinity disturbs overall plant growth in legumes (Fig. 1; Flexas et al., 2004; Murillo-Amador et al., 2007) by influencing the complex interaction of hormones, nutritional imbalances, specific ion toxicity and osmotic effects (Yadav et al., 1989; El Sayed, 2011). Salinity has strong and diverse effects on the overall plant growth, grain yield, and quality and composition of grains (López-Aguilar et al., 2003; Manchanda and Garg, 2008). For instance, photosynthesis in legumes decreases under salt stress due to the short supply of CO_2 and/or salinity-induced reductions in photosynthetic pigments and disturbance in electron transport activity of photosystem II (PS II). Reduced availability of CO_2 is caused by limitations in diffusion through stomata while the reduction in photosynthetic pigments and electron transport activity of PS II are caused by specific ion toxicity from over-accumulated Na^+ and/or Cl^- and/or salinity-induced oxidative stress (Flexas et al., 2004; Khan et al., 2015, 2016a, b). Increased chlorosis and necrosis of leaves are often observed under salt stress, which trigger leaf senescence in legumes (Sehrawat et al., 2013a, b). Likewise, grain protein contents in grain legumes decline under salt stress due to reduced nitrate (NO_3^-) absorption from the soil solution and/or disturbed N metabolism (Ghassemi-Golezani et al., 2010).

The impact of salt stress on several crops has been reviewed (Flowers et al., 2010; Deinlein et al., 2014; Farooq et al., 2015; Parihar et al., 2015), but no comprehensive review is available on the impact, tolerance mechanisms and management of salt stress in grain legumes. In this manuscript, the effects of salt stress on seedling emergence, leaf development, senescence, carbon fixation and light harvesting, hormonal regulation, nutrient uptake, and grain development in grain legumes are reviewed and resynthesized. The mechanisms of salt tolerance are described. Moreover, other management strategies, as well as newly developed breeding and functional genomics approaches to improve tolerance against salt stress in grain legumes are discussed.

2. Effect of salt stress on grain legumes

Grain legumes are sensitive to salinity stress which substantially reduces yield (Table 1). Salinity poses a severe threat to germination and plant growth, the symbiotic association with *Rhizobium*, root nodule development, and the capacity to fix nitrogen in legumes (van Hoorn et al., 2001).

A salinity-induced yield reduction is associated with reduced carbon fixation (Flexas et al., 2004), disturbed hormonal regulation, nutritional imbalances, specific ion and osmotic effects (Yadav et al., 1989; El Sayed, 2011), delayed flowering, and reduced flower numbers and pod set (Khan et al., 2016a). Salt stress effects on seed germination, seedling establishment, nutrient uptake, carbon fixation and light harvesting, and grain yield and quality in legumes are highlighted below.