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REVIEW



Mechanisms of salt stress tolerance in *Casuarina*: a review of recent research

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ABSTRACT

Salinization is a global concern whose extent is predicted to progressively increase over this century. In this context, biosaline agriculture has been included in the set of climate-smart solutions to support sustainable and resilient ecosystems. The Casuarinaceae family is widely known for its intrinsic ability to thrive under saline environments. Therefore, understanding the mechanisms underlying salt-tolerance in this family is of utmost importance for landscape integration and soil rehabilitation. In this mini-review, we present the state of the art of *Casuarina* research – from gene to ecosystem – in response to salinity, towards green growth and sustainable development. Based on literature retrieval from 2000 to 2021, a general overview of salt-stress tolerance in the Casuarinaceae is presented, and the extent of the contribution of root-nodule and arbuscular mycorrhizal symbioses, as well as the related eco-physiological and molecular changes are discussed.

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Introduction

Soil salinization and sodification are widespread soil degradation (and desertification) processes (Butcher et al. 2016). Saline soils contain high levels of soluble salts, imposing limitations on plant water uptake, while sodic soils are enriched in sodium ions that alter the soil structure, leading to soil compaction and reducing water flow. Salt-induced land degradation is linked to climate and anthropogenic drivers (FAO and ITPS 2015) and may have an economic cost up to USD 400 ha⁻¹ (Munns and Gilliam 2015). Additionally, in less than 30 years, i.e. by 2050, global agricultural systems must feed ca. 10 billion people, demanding an increase of food production of 70% in a scenario of climate extremes, rising seawater levels, and a reduction of arable land higher than 50% (WMO 2019). In this context, the use of saline water and halophytes is an alternative strategy to overcome the projected food and environmental crisis.

Actinorhizal plants belonging to the Casuarinaceae family have been widely reported to thrive in extreme environments, namely under drought and hot conditions, in coastal sandy-saline soils (see, e.g. Tanaka 2009). Therefore, the analysis of salt-tolerance mechanisms in this family is crucial to assess the ecological potential of *Casuarina* species for landscape integration and soil rehabilitation. This mini-review compiles results of *Casuarina* salt-stress research developed worldwide, with particular emphasis in the last two decades, when this issue was consistently brought forward.

Resilience of *Casuarina* to saline environments

Although many *Casuarina* species can be considered true halophytes, there is a wide spectrum of responses and tolerance levels. For example, in India *C. glauca* (CSIRO seed lots

13987 and 13144), *C. obesa* (13162 and 13218), and *C. equisetifolia* (14196), presented survival rates of 77%, 52%, and 43%, respectively, in saline waterlogged soils (Tomar and Gupta 2002). Moderate to high survival rates were also observed in saline soils from Australia (Carter et al. 2006a) and Tunisia (Souguir et al. 2019) for *C. obesa* (seed lots from Austin Bay Nature Reserve) and *C. glauca* (seed lots from the Regional Commission for Agricultural Development of Ariana), respectively. Indeed, several studies performed under controlled experimental conditions, revealed that several ecotypes of these *Casuarina* species, including Australian seed lots from CSIRO, and Indian clones from the germplasm collection of the Institute of Forest Genetics and Tree Breeding, may tolerate nearly seawater levels of salt (Van der Moezel et al. 1989; Carter et al. 2006a, 2006b; Isla et al. 2014; Batista-Santos et al. 2015; Selvakesavan et al. 2016; Djighaly et al. 2018; Diagne et al. 2020). However, while *C. glauca* was able to sustain growth and biomass in sodic soils, *C. obesa* was negatively impacted by the same type of soils (Goel and Behl 2005). Additionally, *C. glauca* and *C. equisetifolia* have been used since decades to ameliorate sodic soils in India (Batra and Dikshit 1994; Singh et al. 2011, 2019; Seenivasan et al. 2016).

However, salt tolerance does not seem to align with sodicity tolerance. Van der Moezel et al. (1989) reported salt tolerance (under well-drained conditions) in decreasing order for *C. obesa* > *C. cristata* > *C. glauca* > *C. equisetifolia* var. *incana* > *C. equisetifolia* var. *equisetifolia* > *C. cunninghamiana*. Marcar (1996), on the other hand, reported salt tolerance in decreasing order for *C. obesa* > *C. glauca* > *C. equisetifolia* > *C. cunninghamiana* > *C. cristata*. These data clearly highlight the importance of the choice of ecotype and not just plant species. Nevertheless, the potential of the use of actinorhizal plants in saline

agriculture or agro-forestry is yet poorly understood as research on the topic emerged quite recently and has been more concentrated on the elucidation of the mechanisms associated with salt-tolerance.

Contribution of root symbioses to salt-tolerance in *Casuarina*

The contribution of root symbioses with *Frankia* and/or with mycorrhizal fungi is highly dependent on plant age and ecotype, as well as on the microbial strain. Seedlings of *C. equisetifolia* (seed lots from JIRCAS Okinawa Subtropical Station, Japan) were able to tolerate levels of NaCl up to 500 mM only when inoculated with *Frankia* Ceq1, although both plant and *Frankia* were considered highly tolerant to salt (Tani and Sasakawa 2003). Based on the results of Na⁺ accumulation in plant shoots (up to 300 mM in plants subjected to 500 mM NaCl) and roots (up to 150 mM) as well as on bacterial cells (up to 30 mM), the authors hypothesize that *C. equisetifolia* has effective mechanisms to mitigate the deleterious effects of Na⁺, while *Frankia* prevents the influx of Na⁺ through structural modifications of hyphae. On the other hand, Selvakesavan et al. (2016) reported contrasting salt tolerance in young plants of 82 *C. equisetifolia* clones (Institute from Forest Genetics and Tree Breeding, Coimbatore, India), 17 of which tolerating up to 550 mM NaCl with survival rates of 60 to 95%, and 13 considered salt sensitive (0 to 40% survival). The accumulation and shoot/root ratio of Na⁺, together with the accumulation of proline in the tolerant clones, may indicate multiple levels of stress tolerance mechanisms like vacuolar sodium sequestration and osmoprotection (Selvakesavan et al. 2016). Similarly, *C. glauca* seedlings from an Egyptian ecotype nodulated by *Frankia* CcI156 and CgIM4 were able to withstand up to 200 mM NaCl, with a more prominent contribution of CgIM4 (Mansour et al. 2016), while young plants (seeds from www.nzseeds.co.nz) tolerated up to 600 mM NaCl. On the other hand, *Frankia casuarinae* strain Thr (Hurst et al. 2014) did not enhance salt tolerance of young *C. glauca* plants (seeds from www.nzseeds.co.nz), likely associated with an intrinsic plant ability to cope with stress (Batista-Santos et al. 2015; Jorge et al. 2021). However, this might be due to the fact that *F. casuarinae* strain Thr showed low salt tolerance *in planta* (Duro et al. 2016; Ribeiro-Barros et al. 2016). Inoculation of young *C. glauca* plants (Myall Lakes National Park, Australia), grown in hydroponic nutrient solution, with *Frankia* CcI3 or CeD enhanced salt stress tolerance up to 200 mM NaCl, with a more pronounced positive effect of CcI3. In the case of young plants of *C. equisetifolia* (Louga, Senegal) grown on soil, only *Frankia* CeD produced a visible effect (Ngom et al. 2016).

Similarly, salt tolerance of the same *C. glauca* and *C. equisetifolia* ecotypes in symbiosis with arbuscular mycorrhizal fungi (AMF) was dependent on the fungal strain, with a clear positive effect of *Rhizophagus fasciculatus* strain DAOM227130 (Rf) (Djighaly et al. 2018). This effect was enhanced by co-inoculation with both *Frankia* CeD and Rf (Djighaly et al. 2018). The same was observed in young plants of *C. obesa* whose salt tolerance was enhanced to concentrations up to 300 mM NaCl upon inoculation either with plant growth promoting bacteria (PGPB) or with AMF, as well as by co-inoculations with both PGPB and AMF (Diagne et al. 2020). This phenomenon, related with

a strong ability of well-chosen PGPB and AMF to mitigate different abiotic stress factors, has long been observed for herbaceous crop plants (Egamberdieva et al. 2019; Dastogeer et al. 2020), and therefore it is not surprising that it also works for trees. However, long-term studies on microbial competition in the soil are required to find out which PGPB and AMF can provide stable support. *Frankia* strains, once established in nodules, will be less vulnerable to competition.

Mechanisms underlying salt-tolerance

The reported ecophysiological adjustments leading to salt tolerance in the Casuarinaceae are mostly related to ion exclusion in the leaves and/or sequestration in the roots, maintenance of high relative water content (RWC), osmotic adjustments and enhanced control of oxidative conditions, as well as maintenance of membrane integrity and the potential of the components involved in the carbon assimilation pathway. For example, in *C. obesa*, the tolerance to high salinity levels was related to the exclusion of ions (Carter et al. 2006a; Isla et al. 2014), osmotic adjustments, accumulation of compatible organic solutes, and photoprotective mechanisms (Carter et al. 2006a,b). Accordingly, ion extrusion (Fan et al. 2018; Gupta et al. 2018) and osmolyte accumulation (Tani and Sasakawa 2006) were also implicated as important salt tolerance mechanisms in *C. equisetifolia*. In this species, ion translocation to shoots and retention in roots were observed, suggesting the existence of alternative mechanisms to protect cells from Na⁺ (Selvakesavan et al. 2016). Indeed, in a recent study Wang et al. (2021) reported that the usual root epidermal cells were replaced by a compact layer of cells and potassium concentration remained stable. The same authors reported that differentially expressed genes (DEGs) of the root transcriptome from *C. equisetifolia* exposed to 200 mM NaCl, were mostly related to oxidative stress and detoxification, Na⁺/H⁺ and K⁺ transport, and potassium channel proteins, and upregulated in response to salt stress. Additionally, as the stress imposition progressed an enrichment of DEGs involved in apoptosis and transcriptional regulation (*WRKY* and the *MYB* genes) families was also observed.

In *C. glauca* an integrated analysis of salt tolerance (including the contribution of *Frankia* symbiosis) has been performed by our team. This was mainly centered in the branchlets and included, ecophysiological studies (Batista-Santos et al. 2015; Duro et al. 2016), evaluation of membrane lipid remodeling (Scotti-Campos et al. 2016), metabolomics (Jorge et al. 2017a, 2017b, 2019, 2021), and proteomics (Graça et al. 2020). According to Batista-Santos et al. (2015), despite the decrease in plant growth and the accumulation of Na⁺ and Cl⁻ ions in branchlets of *C. glauca* exposed to increasing levels of NaCl up to 600 mM, the RWC decreased only ca. 10%, accompanied by a sharp reduction of the osmotic potential. This suggests that osmotic adjustments were necessary for the acclimation response. Additionally, the authors observed that *C. glauca* plants were able to activate photoprotective mechanisms, slightly reducing the levels of key photosynthetic and respiratory enzymes (without inactivation), enhancing the antioxidative response and producing osmoprotectant solutes. On the other hand, membrane permeability and the unsaturation degree of membrane lipids remained mostly unchanged (Scotti-Campos et al. 2016). Complementary, metabolomics of salt

stress revealed the importance of the secondary metabolome, namely of the flavonoid-based antioxidant system (Jorge et al. 2019) in complementing the increased activity of enzymatic scavengers of reactive oxygen species (ROS) associated with the ascorbate-glutathione cycle (Scotti-Campos et al. 2016; Jorge et al. 2017a, 2021). This highlights the importance of both enzymatic and non-enzymatic scavenging components in the control of oxidative stress and, thereby, their key role in stress tolerance enhancement. However, it should be noted that the concomitant presence of heat stress (45°C) might jeopardize *C. glauca* acclimation to salinity (400 mM NaCl), due to a negative heat and salt interaction that aggravated stress severity (Jorge et al. 2021). The analysis of the proteome of *C. glauca* branchlets corroborated the previous studies, highlighting the robustness of tolerance to single salt stress exposure in this species (Graça et al. 2020). Indeed, the overall set of proteins is quite stable, even at salt concentrations of 400 or 600 mM NaCl, with a remarkable accumulation of multifunctional key proteins involved in photosynthetic metabolism (e.g. quinone-oxireductase, thylakoid luminal 19 kDa protein); protection against oxidative stress (e.g. monodehydroascorbate reductase, ascorbate and thioredoxin-dependent peroxidases, and superoxide dismutase); glycolysis and TCA cycle (e.g. glyceraldehyde-3-phosphate dehydrogenase, cytosolic NADP-malic enzyme, NAD-dependent malate dehydrogenase); and general stress response (e.g. lipocalin, annexin, allene oxide cyclase, universal-stress protein, thaumatin-like protein, cyclophilin). The associated Protein-Protein Interactions (PPI) involve two major networks, one comprised by interacting proteins involved in metabolic pathways and biosynthesis of secondary metabolites, and the other by proteins involved in protein processing and export, carbon metabolism, and peroxisomal metabolism.

Altogether, data integration strongly points to a robust constitutive defense mechanism of *Casuarina* against various stresses and to the activation of defense responses during the early stages of stress imposition.

Concluding remarks

Depending on the ecotype, *Casuarina* species may tolerate up to seawater levels of salt, and can be included in the group of halophyte plants. However, the ability to cope with salinity is highly dependent on the plant species, age and ecotype. The contribution of root-nodule symbiotic *Frankia*, AMF and PGPB may enhance the intrinsic plant tolerance, particularly at the seedling stage, but it depends on the plant-bacteria or plant-AMF genotype combination. The selection of PGPB consortia to enhance plant performance holds great potential for increasing the use of *Casuarina* species. However, salt stress research has yet many gaps to bridge, among them, (i) standardization of the experimental assays that mimic field conditions as much as possible; (ii) inclusion of adult plants in the experimental analyses; (iii) choice of the best combinations plant ecotype – bacterial and/or fungal strains, for specific geographical locations; (iv) high-throughput analysis (genomics, transcriptomics, proteomics and metabolomics) of branchlets, roots, and symbiotic organs, which must be integrated with ecophysiological and biochemical data associated with the acclimation, resilience and performance of the plant. Finally, taking into account the challenges imposed by climate change and human population growth, the provision of

ecosystem services by Casuarinaceae must more than ever not be forgotten. Among others, attention should be paid at the potential of *Casuarina* spp. for the following purposes: (i) protection of coastal zones, which is an effective way to mitigate the impact of extreme events (like in the case of the 2004 tsunami in the Philippines); (ii) growth on saline/waterlogged wastelands; (iii) biomass production and carbon sequestration; (iv) production of renewable energies; and (v) integration in agroforestry systems.

Disclosure statement

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