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Research article

Ecophysiological adaptations of two halophytes to salt stress: Photosynthesis, PS II photochemistry and anti-oxidant feedback – Implications for resilience in climate change

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ABSTRACT

Halimione portulacoides and *Sarcocornia fruticosa* commonly exhibit a reddish coloration especially in high evaporation periods, due to betacyanin production in response to stress. Although sharing the same area in salt marshes, they present different strategies to overcome salinity stress. While *S. fruticosa* present a dilution strategy, increasing succulence, *H. portulacoides* appears to have developed an ionic compartmentalization strategy. Nevertheless, there's still a decrease in the photosynthetic activity in different extents. While in *S. fruticosa*, the impairment of photosynthetic activity is due to a decrease in the flow from the electron transport chain to the quinone pool; in *H. portulacoides* the process is affected far more early, with high amounts of energy dissipated at the PSII light harvesting centers. This photosynthetic impairment leads to energy accumulation and consequently to the production of reactive oxygen species (ROS). SOD was particularly active in stressed individuals, although this increment is rather more significant in *S. fruticosa* than in *H. portulacoides* suggesting that *H. portulacoides* may have a maximum salt concentration at which can sustain cellular balance between ROS production and scavenging. These different ecophysiological responses have great importance while evaluating the impacts climate change driven increase of sediment salinity on halophyte physiology and on the marsh community and ecosystem services.

1. Introduction

A decrease in photosynthesis capacity is very common in salt stressed plants [24,36,37,42], mostly due to a low osmotic potential of the soil solution (osmotic stress), specific ion effects (salt stress), nutritional imbalances or more usually, a combination of these factors [57]. Similarly to other stress factors, these induce plant biochemical and physiological disturbances [37]. One of the consequences of salinity induced limitation of photosynthetic capacity, is the exposure of plants to excess of energy with inevitable consequences on the photosystem II (PSII), if the dissipation mechanisms are not efficient enough [12,42], since plants under salt stress use less photon energy for photosynthesis [34]. The effects of salinity on photosynthesis include several other consequences besides the damage on PSII. Also the photosynthetic carbon harvesting is affected by disturbances on leaf water relations and osmotic potential [37,55], on the chloroplast membrane systems and on the pigment composition (carotenoids and chlorophyll). To avoid damages to the PSII, plants have developed several strategies to dissipate excessive energy, protecting the photosynthetic apparatus. One of these mechanisms is the dissipation of energy throughout the xanthophyll cycle already described for several photosynthetic organisms as a stress response mechanism [12,19,29]. During this cycle, excessive energy is dissipated in the form of heat through the formation of zeaxanthin by de-epoxidation of violaxanthin via antheraxanthin [44].

Halophytes typically are considered to be plants able to complete their life cycle in environments where the salt concentration is around 200 mM NaCl or higher, representing 1% of the world flora [13]. *Halimione portulacoides* and *Sarcocornia fruticosa* are two Amaranthaceae widely distributed on the Portuguese and European salt marshes. They present different strategies against salt stress. While *H. portulacoides* has specific salt glands on the leaves to excrete the excess of salt, *S. fruticosa* increases its water content in the photosynthetic stems, becoming turgid and this way promotes salt dilution [30]. Also their photosynthetic pathways differ

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substantially, being *H. portulacoides* a C3 plant while *S. fruticosa* is described as a CAM organism [43].

Considering these differences of defence against salt stress and on the photosynthetic mechanisms, this study aims to investigate *in situ* how the photosynthesis of these halophytes is affected when under salt stress and how this will affect the carbon sequestration rates, in order to understand the defence and tolerance mechanisms towards salt stress.

2. Results

2.1. Leaf elemental content

All stressed individuals showed higher Na concentrations (Fig. 1) in the photosynthetic tissues, independently from the analysed specie. When comparing both species, stressed *H. portulacoides* individuals presented higher concentrations of Na when compared with *S. fruticosa* stressed individuals. In which concerns the non-stressed individuals, the opposite trend could be verified, with higher Na concentrations in the photosynthetic organs of *S. fruticosa*. Concerning K, the exact same pattern was observed between species, although with higher concentrations in non-stressed individuals. Calcium exhibited a distinct pattern between species. While in *S. fruticosa* Ca content was higher in non-stressed individuals, in *H. portulacoides* the higher concentrations were observed in stress individuals.

2.2. Leaf water status

Leaf relative water content (Fig. 2) showed both differences between species and within the same specie between stressed and non-stressed individuals. *S. fruticosa* stressed individuals showed lower water contents than the non-stressed ones, while in *H. portulacoides* the opposite behaviour was observed, with higher water contents in the individuals subjected to higher salinities. Beside this, *S. fruticosa* had slightly higher water content than *H. portulacoides*, under normal circumstances.

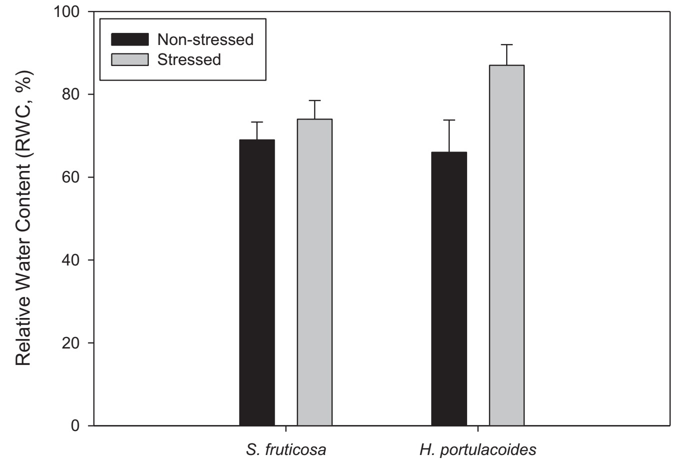

Fig. 2. Leaf relative water content (RWC) in stressed and non-stressed individuals of *S. fruticosa* and *H. portulacoides* species (average ± standard deviation, $n = 10$).

2.3. Photosynthetic gas exchange and PSII activity

Independently of their stress levels, *S. fruticosa* individuals showed always-higher gas exchange rates than *H. portulacoides* (Fig. 3). Comparing the stressed individuals with the non-stressed,

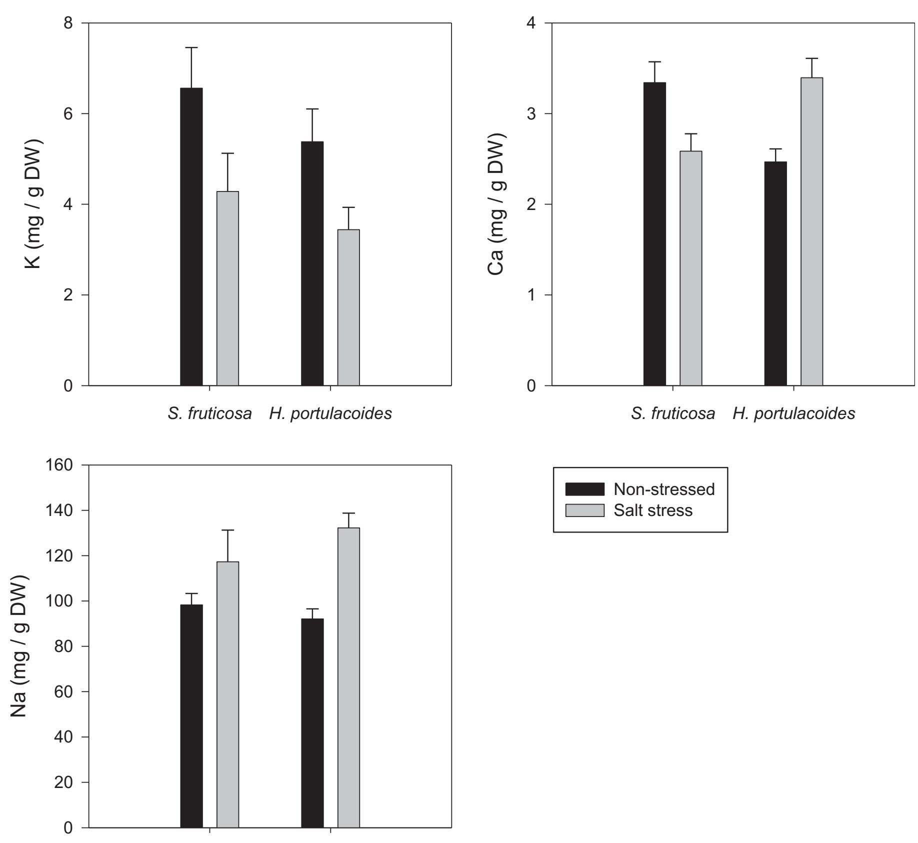

Fig. 1. Potassium, Calcium and Sodium leaf concentrations in stressed and non-stressed individuals of *S. fruticosa* and *H. portulacoides* species (average ± standard deviation, $n = 10$).