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Comparison of salinity tolerance of three *Atriplex* spp. in well-watered and drying soils☆

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ABSTRACT

Members of the Chenopodiaceae are well adapted to both salt and drought stress and can serve as model species to understand the mechanisms of tolerance in plants. We grew *Atriplex hortensis* (ATHO), *A. canescens* (ATCA), and *A. lentiformis* (ATLE) along a NaCL salinity gradient under non-water-limited conditions and in drying soils in greenhouse experiments. The species differed in photosynthetic carbon fixation pathway, capacity for sodium uptake, and habitat preferences. Under non-water-limited conditions, ATLE (C4) maintained high growth rates up to 30 g L^{-1} NaCl. ATHO (C3) had lower growth than ATLE at high salinities, while ATCA (C4) grew more slowly than either ATLE or ATHO and showed no net growth above 20 g L^{-1} NaCl. ATHO and ATLE accumulated twice as much sodium in their shoots as ATCA, but all three species had increasing sodium levels at higher salinities. Potassium, magnesium and calcium levels were relatively constant over the salinity gradient. All three species showed marked accumulation of chloride across the salinity gradient, whereas nitrate, phosphorous and sulfate decreased with salinity. The effect of drought was simulated by growing plants in sealed pots with an initial charge of water plus NaCl, and allowing them to grow to the end point at which they no longer were able to extract water from the soil solution. Drought and salinity were not additive stress factors for *Atriplex* spp. in this experiment. NaCl increased their ability to extract water from the soil solution compared to fresh water controls. ATLE showed increased shoot dry matter production and increased water use efficiency (WUE) as initial salinity levels increased from 0 to 30 g L^{-1} NaCl, whereas dry matter production and WUE peaked at 5 g L^{-1} for ATHO and ATCA. Final soil moisture salinities tolerated by species were 85 g L^{-1}, 55 g L^{-1} and 160 g L^{-1} NaCl for ATHO, ATCA and ATLE, respectively. C4 photosynthesis and sodium accumulation in shoots were associated with high drought and salt tolerance.

1. Introduction

1.1. Need for understanding the physiology of drought and salt tolerance in well-adapted plants

Water and salt stress frequently co-occur in both natural and agricultural ecosystems, because as soils dry salts become concentrated in the remaining soil solution (Munns, 2002; Chaves et al., 2009). Numerous studies have investigated drought and salt stress separately but fewer have examined their interactions. While most studies have been conducted with crop plants, it is also important to investigate the physiology of salt and drought tolerance in well-adapted wild plants, to understand the limits and trade-offs between drought and salt tolerance, and the traits that are associated with high tolerance to both factors. Well-adapted wild plants are potential new crop plants (Glenn et al., 1999; Rozema and Flowers, 2009), and can also serve as model systems for improving the drought and salt tolerance of conventional crops (Flowers, 2004; Flowers and Colmer, 2008).

1.2. Interaction between drought and salinity stress

Drought and salinity are often regarded as additive stress factors for plants (e.g., Munns, 2002; Chaves et al., 2009). For example, agricultural models typically treat them as separate factors contributing to reduced crop yield (e.g., Letey et al., 1985; Letey and Dinar, 1986; Bresler and Hoffman, 1986; Cardon and Letey, 1994). However, Shani and Dudley (2001) and Dudley et al. (2008), studying a variety of crops deficit-irrigated with saline water, found that salinity actually had a protective effect on plant yield under

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water-limited conditions. They developed a model in which plant water uptake and growth occurred up to the salt tolerance limit of the crop, with crops preferentially extracting water from the lowest salinity portion of the root zone (i.e., the upper part of the root zone), and water above the salinity tolerance limit exiting the root zone as a leaching fraction. This model was subsequently supported by Letey et al. (2011) in a re-evaluation of the existing literature on crop-salinity interactions, resulting in much lower recommended leaching requirements for maintaining crop yield under saline irrigation.

Similar results have been reported for halophytes. As examples, growth enhancement by NaCl for plants under water stress have been noted for the halophytes *Sesuvium portulacastrum* (Slama et al., 2008a,b) and *Spartina alterniflora* (Brown et al., 2006). Uaeda et al. (2003) grew sea aster (*Aster tripolium*) on 0 mM NaCl and 300 mM NaCl in soils with or with imposed water stress, and found that NaCl prevented the desiccation of leaves observed on water-stressed plants grown without NaCl. One mechanism by which response to salinity enhances drought tolerance is through an increase in water use efficiency (WUE) via reduced stomatal conductance; this leads to slower growth, but an increase in the ratio of carbon fixed per unit of water transpired, as reported for *A. canescens* (Glenn and Brown, 1998). *A. lentiformis* (Zhu and Meinzer, 1999) and *A. halimus* (Alla et al., 2011).

1.3. Experiments to determine interactions of salinity and water stress in plants

Designing experiments to co-vary salinity and water-stress can be difficult. Tolerance to salinity can be determined by irrigating plants with solutions varying in salt concentration at frequent intervals (e.g. daily) with enough water to flush excess salts from the soil so that salinity in the root zone is close to the salinity of the irrigation solution (Glenn and O'Leary, 1984; Flowers and Colmer, 2008). Water-stress can be imposed by irrigating plants with restricted amounts of water to maintain the soil moisture level at a given fraction of field capacity (e.g., Uaeda et al., 2003; Slama et al., 2008b). However, in this type of experiment salts will differentially concentrate in the pots over time in the absence of a leaching fraction, confounding the ability to keep a constant salt concentration at a given water-stress treatment.

Many other studies have used polyethylene glycol (PEG), a high-molecular-weight polymer, to simulate drought by imposing osmotic stress on plants. Examples of studies with halophytes are in Alla et al. (2011), Ben Hassine et al. (2008), Martinez et al. (2003). Mannitol has also been used to impose osmotic stress (Slama et al., 2008a). However, PEG and mannitol can be taken up by plants, possibly interfering with their growth characteristics; furthermore, hydroponic experiments in which PEG or mannitol are added to the nutrient solution do not adequately reproduce the complex root–soil–water interactions that occur in drying soils (e.g., Barrow and Osuna, 2002).

1.4. Objectives of the present study

This study tested the interaction between salinity and water stress in three *Atriplex* species differing in photosynthetic pathway and capacity to accumulate sodium. The goals were to determine physiological traits associated with high drought and salt tolerance, and the interactions between salinity and drought stresses in well-adapted plants. *A. lentiformis* (ATLE) is a North American C4 phreatophytic desert riparian shrub. It is a high-sodium halophyte capable of high yields under seawater irrigation (Glenn and O'Leary, 1985), but it also grows in less saline and more xeric conditions in inland sites (Blank et al., 1998). *A. hortensis* (ATHO) is an annual, European C3 species adapted to brackish marshes in temperate environment. It is a sodium-accumulating, halophytic species capable of growing on seawater (Stelter and Jeschke, 1983; Jeschke and Stelter, 1983; Wilson et al., 2000). *A. canescens* var. *angustifolia* (Torr.) S. Wats. (ATCA) is a drought-adapted, low-sodium, desert variety of this North American C4 shrub (Glenn et al., 1998; Sanderson and Stutz, 1994), exhibiting moderate salt tolerance compared to salt marsh varieties of *A. canescens* (Glenn et al., 1992a,b).

ATLE and ATCA are important rangeland and forage crops (Watson and O'Leary, 1993; Howard, 2003; Meyer, 2005), while ATHO is grown as a green vegetable crop (Carlsson, 1980; Shannon and Grieve, 1999). Our working hypotheses were: degree of salt tolerance would be correlated with capacity for sodium uptake; tolerance to water stress would be correlated with photosynthetic pathway; and salinity would confer a protective effect on water stress tolerance, as observed for other halophytes.

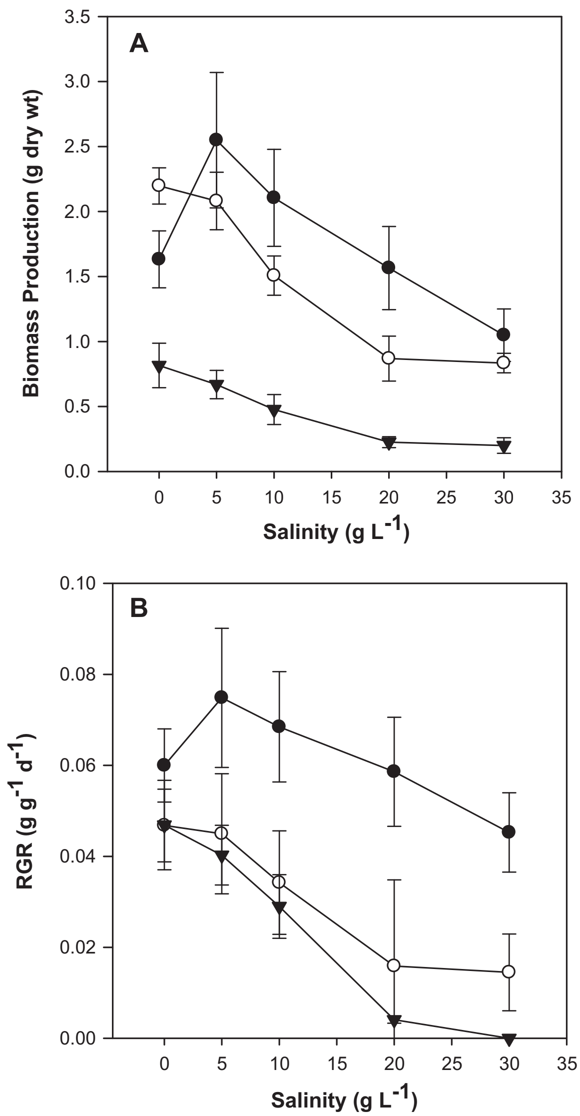

Fig. 1. Shoot dry biomass (A) and relative growth rates (RGR) (B) for ATLE (closed circles), ATHO (open circles) and ATCA (closed triangles) grown along a salinity gradient under well-watered conditions in a greenhouse experiment in Tucson, Arizona. Error bars are standard errors of means.