



Photosynthesis, stomatal responses, and water potential in three species in an inland salt marsh in Kansas, USA

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ABSTRACT

Interspecific variation of photosynthesis and water potential in inland salt marsh species has been largely unexplored. In this study, photosynthesis and water potential were measured in individuals of *Spartina pectinata* Link, *Distichlis spicata* (L.) Greene, and *Bolboschoenus maritimus* (L.) Palla in an inland salt marsh, possibly the first field measures of photosynthesis in inland salt marsh plants in North America. It was hypothesized that the C₄ grasses *S. pectinata* and *D. spicata* would have a greater tolerance to salinity compared to the C₃ sedge *B. maritimus* by stomata being less responsive to changing water status. During the study, *B. maritimus* was most sensitive to dry conditions, which was manifested as low photosynthesis, stomatal conductance, and water potential. Stomatal closure occurred in all species under dry conditions, but particularly in *B. maritimus*. Under dry conditions, *S. pectinata* maintained higher photosynthesis compared to other species. Water potential was lower in *D. spicata* compared to the other species. There were significant correlations between plant water potential and photosynthesis and water potential and stomatal conductance in *B. maritimus*, but not in *S. pectinata* or *D. spicata*. This is evidence of sensitivity of *B. maritimus* to dry conditions and tolerance in *S. pectinata* and *D. spicata*, largely due to stomatal responses.

1. Introduction

Plant water relations can influence the environmental boundaries in which a plant can survive (Engels and Jensen, 2010; Engels et al., 2011; Hester et al., 2001). Measures of photosynthesis and water potential are especially meaningful in saline systems, as water is difficult to absorb from salty soil (Maricle et al., 2007a). How plants respond to salinity, and the relevant adaptations or acclimations, are of great interest in ecology and evolutionary biology (Cheeseman, 2015; Negrão et al., 2017; Shabala, 2013).

One common physiological response to salinity is closure of stomata, but this does not always influence photosynthesis (Mateos-Naranjo et al., 2010; Negrão et al., 2017). Stomatal influences on photosynthesis relate to leaf internal availability of CO₂ (Farquhar and Sharkey, 1982), which differs between C₃ and C₄ plants (Long, 1999). The CO₂ concentrating mechanism of C₄ plants makes photosynthesis largely independent of stomatal conductance (g_s) (Ghannoum, 2009; Huxman and Monson, 2003; Taylor et al., 2011). By contrast, CO₂ uptake in C₃ plants is more sensitive to changes in g_s (Álvarez et al., 2012; Flanagan and Jefferies, 1988; Liu and Shi, 2010; Redondo-Gómez

et al., 2006, 2007), which can become important in environmental conditions where water is limiting.

Numerous physiological factors can reduce photosynthesis in water-stressed (including salinity-stressed) plants, which can be categorized into stomatal and non-stomatal limitations (Maricle and Adler, 2011). Stomatal limitations on photosynthesis result from a closure of stomata that restricts access to CO₂ in the leaf (Farquhar and Sharkey, 1982). Decreased stomatal conductance has been shown to limit photosynthesis in some C₃ plants (Álvarez et al., 2012; Brugnoli and Björkman, 1992; Flanagan and Jefferies, 1988; James et al., 2002; Liu and Shi, 2010; Redondo-Gómez et al., 2006, 2007), but C₄ photosynthesis is more commonly decreased by non-stomatal limitations during water stress (Ghannoum, 2009; Maricle et al., 2007b, 2015, 2017; Shahbaz et al., 2011; Soares-Cordeiro et al., 2009). Non-stomatal limitations to photosynthesis during salinity can include decreased chlorophyll concentration (James et al., 2002), ion accumulation to toxic levels (Shabala, 2013), decreased photosynthetic enzyme activity (Chaves et al., 2009; Soares-Cordeiro et al., 2009), or increased oxidative stress that comes with salinity (Maricle et al., 2007a). Determining whether reductions in photosynthesis occur as a result of stomatal or non-

Abbreviations: ANOVA, analysis of variance; C_i, internal (intercellular) CO₂ concentration; g_s , stomatal conductance to water vapor; P_{max} , maximum rate of photosynthesis when light saturated; Ψ , water potential

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stomatal limitations can be determined with measures of internal (intercellular) CO₂ concentration (C_i) (Farquhar and Sharkey, 1982). If stomatal closure limits photosynthesis, C_i is drawn down as CO₂ in the leaf becomes limiting (Maricle and Adler, 2011). Therefore, decreased C_i indicates stomatal limitations on photosynthesis (Farquhar and Sharkey, 1982).

Salinity affects plants both by toxic ion effects and also by osmotic effects in soil, which makes it difficult for plants to absorb water (Maricle et al., 2007a). Osmotic effects of salinity on plants can be assessed with measures of water potential (Ψ). Numerous factors can influence Ψ, including dry soils and salinity (Maricle et al., 2007a). Saline soils are characterized by low Ψ owing to a large number of solute particles (Campbell and Norman, 1998). Consequently, one aspect of salt tolerance in plants is an ability to make Ψ in roots more negative compared to a plant that is more sensitive to saline soils (Álvarez et al., 2012; Casolo et al., 2015; Krüger and Kirst, 1991). Mid-day measures of plant Ψ indicate plant water status during the time of day with the greatest water stress on a plant (Maricle and Adler, 2011), illustrating the extent to which a plant can adjust to dry or saline soils.

Although interspecific variations of photosynthesis and water potential in relation to salinity have been measured extensively in coastal marsh species (e.g., Castillo et al., 2005; Di Bella et al., 2016; Drake, 1989; Hester et al., 2001; Kemp and Cunningham, 1981; Krüger and Kirst, 1991; Mateos-Naranjo et al., 2013; Pezeshki et al., 1987; Redondo-Gómez et al., 2006, 2007; Touchette, 2006; Touchette et al., 2009; Warren and Brockelman, 1989), these measures have been largely unexplored in inland salt marshes. Few studies have explored physiology of inland salt marsh plants (Aschenbach, 2006; Caudle and Maricle, 2015; Koyro et al., 2013; Marchesini et al., 2014; Mishio and Kachi, 1998; Redondo-Gómez et al., 2014), and none of these studies measured photosynthesis *in situ* for salt-affected plants. Inland salt marshes tend to be more unpredictable than coastal marshes when considering water input (Marchesini et al., 2014), and plants living there might be more subjected to conditions of drought compared to plants in coastal marshes. The present study is possibly the first to present field measures of photosynthesis in inland salt marsh plants in North America. Here, C₃ and C₄ species were compared in a Kansas (USA) salt marsh to determine if the C₄ species are better adapted to survive in a saline environment during a dry season.

It was hypothesized that photosynthesis in the C₄ grasses *Spartina pectinata* Link and *Distichlis spicata* (L.) Greene would be more tolerant of saline soils compared to the C₃ sedge *Bolboschoenus maritimus* (L.) Palla owing to a lower sensitivity of stomatal conductance to changing water potential. These are typical physiological differences between C₃ and C₄ plants, and they might play a role in ecological salt tolerance. In C₄ plants this would manifest itself as higher photosynthesis with lower stomatal conductance. It was also hypothesized that greater sensitivity of photosynthesis in the C₃ species to salt would be evident due to greater sensitivity of stomata to drier soils, resulting in decreased photosynthesis rates and stomatal closure. A lower sensitivity of stomata in C₄ plants under salinity could provide an ecological advantage when compared to C₃ plants (Long, 1999).

2. Materials and methods

2.1. Site description

Effects of salinity on salt marsh plants were measured in Quivira National Wildlife Refuge near Stafford, Kansas, USA. Quivira National Wildlife Refuge is underlain by the Harper-Salt Plain Formation of Permian age (Whittemore, 1993) that contributes salt deposits that create inland salt marsh habitats. Two large, shallow salt marshes occur at Quivira National Wildlife Refuge, the “Little Salt Marsh” and the “Big Salt Marsh,” with areas approximately 300 and 600 ha, respectively, and water depths from 1.0 to 1.5 m (Harris and Eberle, 2001). Mean annual precipitation at the site is near 710 mm (Sexson and Farley,

2012), although 2012 was abnormally dry, with precipitation 65 to 70 percent of normal (Maricle et al., 2017). On average, 80% of annual precipitation in the area occurs from April through September (Maricle and Adler, 2011), which would result in 568 mm of rainfall in an average growing season. Rainfall stations near the site recorded up to 394 mm of rain during the period 1 April through 30 September, although 100 mm of this rain occurred in one day following the conclusion of these measures. From 1 April to the conclusion of measures on 17 August, local rainfall measures reported up to 243 mm of rain (Supplemental material).

Water in the salt marshes at Quivira National Wildlife Refuge has variable salinity. Source water has chloride concentrations up to 43 g L⁻¹ (Whittemore, 1993). Standing water in the marsh is diluted by rain and surface runoff; marsh waters can have chloride concentrations in the range of 1253–2301 mg L⁻¹ (Harris, 1999), although areas subject to evaporation can have salts concentrated to high levels, with water potentials of surface soils sometimes lower than -40 MPa (DaSilva-Carvalho, 2009). Soil water potentials at rooting depth, however, were measured to be between -1.4 and -2.2 MPa (mean = -1.8 MPa) during June 2012 with a WP4-T Dewpoint Potentiometer (Decagon Devices, Inc.; Pullman, Washington, USA). Equipment problems prevented measures of soil water potentials in July and August, however.

The most abundant species at the site were investigated. The C₄ salt marsh grasses *Spartina pectinata* and *Distichlis spicata* and the C₃ sedge *Bolboschoenus maritimus* were measured in this study during the dry summer of the year 2012. Plants were measured at two sites within Quivira National Wildlife Refuge: the western portion of the Big Salt Marsh (38° 11' 32" N, 98° 32' 19" W) and slightly north of the Little Salt Marsh (38° 06' 13" N, 98° 29' 18" W). At each site, water potential and photosynthesis were measured in three randomly selected individuals of each species in each of June, July, and August of 2012: 3 species × 6 replicates × 3 months = 54 total plants measured. Separate individual plants were measured in each month.

2.2. Gas exchange measures

An LI-6400XT photosynthesis system (Li-Cor Biosciences, Inc., Lincoln, Nebraska, USA) was used to measure photosynthetic light response curves of each plant at nine levels of photosynthetic photon flux density (PPFD) from 0 to 2000 μmol m⁻² s⁻¹ (Maricle and Adler, 2011). Photosynthesis was measured on clear days between the hours of 10:00 and 15:00 during June 5 and 7, July 17 and 27, and August 9 and 17, 2012. Young, healthy leaves were measured for *S. pectinata* and *D. spicata* and the stem was measured for *B. maritimus*. All leaves were fully exposed to sunlight prior to measurement.

Photosynthesis measures were performed in a 2 cm × 3 cm LED leaf chamber, with gas flow at 400 μmol s⁻¹, CO₂ at 385 μmol mol⁻¹, and temperature and humidity near ambient. Ambient temperatures during measurement periods ranged from 21 to 37 °C, with air in the leaf chamber typically 4 to 10 °C above ambient. Ambient relative humidity during measurement periods ranged from 14 to 65%, with air in the leaf chamber typically 5 to 15% below ambient. Photosynthetic CO₂ uptake, stomatal conductance to water vapor (g_s), and internal (intercellular) CO₂ concentration (C_i) were determined at each irradiance (Maricle and Adler, 2011). The maximum measured photosynthesis rate (P_{max}) and maximum measured g_s were noted for each light response curve.

2.3. Water potential measures

A Scholander pressure chamber (Scholander et al., 1965) (model 1000; PMS Instrument Company, Albany, Oregon, USA) was used to measure mid-day water potential (Ψ) of each plant following photosynthesis measures. Mid-day Ψ measures occurred between the hours of 10:00 and 15:00 (Maricle and Adler, 2011).

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