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Does increased salinity reduce functional depth tolerance of four non-halophytic wetland macrophyte species?

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ABSTRACT

Rapid growth in height is an important mechanism used by many emergent wetland macrophytes to withstand water depth increases, particularly in species unable to maintain sufficient rates of photosynthesis and gas exchange for long-term survival underwater. However, increases in salinity can reduce growth rates and above-ground biomass production in non-halophytic macrophytes and this may reduce their inundation tolerance. We tested this hypothesis by comparing growth responses of *Cynodon dactylon* (L.) Pers, *Paspalum distichum* L., *Eleocharis equisetina* C.Presl and *Bolboschoenus caldwellii* (V.J.Cook) Soják at three depths (5, 20 and 60 cm) across four salinity treatments (200, 2500, 5000 and 10 000 mg L^{-1}). Increases in depth had negative effects on the growth of all four species. The three emergent wetland macrophyte species (*P. distichum*, *E. equisetina* and *B. caldwellii*) grew more rapidly, produced more above-ground biomass, and/or maintained positive growth rates at greater depths in the lower salinity treatments than at higher salinities. The terrestrial grass species, *C. dactylon*, displayed negligible growth when waterlogged and where biomass decreased significantly with depth, there were no significant differences in biomass between the salinity treatments. We conclude that increases in salinity reduced the ability of the three emergent wetland macrophyte species to withstand increases in water depth. The potential depth ranges of these species are therefore likely to change within wetlands if salinisation occurs. Specifically, the habitat ranges of these species are likely to contract and shift towards the shallower, less-frequently flooded limits of their current ranges as salinity levels become limiting to growth.

1. Introduction

Increases in salinity are an issue of concern in many coastal wetlands as well as in inland wetlands affected by secondary salinisation (Howard and Mendelssohn, 1999; James et al., 2003; Spalding and Hester, 2007; Jolly et al., 2008). Tidal restoration, rising sea levels and temperatures, reductions in rainfall, anthropogenic disruption of natural drainage routes and storm surges can all lead to temporary or permanent salinity increases in coastal wetlands (Howard and Mendelssohn, 1999; Spalding and Hester, 2007). Fluctuations in water depth at such sites are often accompanied by changes in soil and water salinity that may affect macrophyte growth and survival. Large increases in salinity can lead to localised elimination of non-halophytic macrophyte species. The effects of such large changes in salinity have been examined in many studies and approximate salinity thresholds for mortality have been documented for a variety of wetland macrophytes (e.g. Hart et al., 1990, 1991, 2003; Jolly et al., 2008). However, much less is known about the effects of less pronounced, sub-lethal increases in salinity on macrophyte communities (James et al., 2003; Jolly et al., 2008). While these may not be sufficient to change community composition by eliminating species, some evidence indicates that such increases could modify the habitat ranges of non-halophytic macrophyte species within wetlands by reducing their tolerance to inundation stress (Morris and Ganf, 2001; Salter et al., 2008).

Inundation reduces the availability of light and atmospheric gases to plants and species differ in their ability to overcome these resource restrictions (Keddy, 2010). Within wetlands, macrophyte species display zonation, largely determined by their inundation tolerance limits (Keddy, 2010). Some wetland macrophyte species maintain sufficient rates of gas exchange and photosynthesis for growth and survival underwater by absorbing dissolved CO_2 directly from the water column, particularly those with submerged

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growth forms (Keddy, 2010). However, emergent aquatic and low-growing terrestrial fringing species often require atmospheric CO_2 and only survive prolonged inundation if a sufficient proportion of the plant remains above the water surface (Rea and Ganf, 1994; Siebentritt and Ganf, 2000). For such species, increased growth in height, sometimes at the expense of below-ground biomass, can be an important mechanism for withstanding increases in water depth (Blanch et al., 1999b; Siebentritt and Ganf, 2000). For example, Siebentritt and Ganf (2000) found that survival of the emergent sedge *Bolboschoenus caldwellii* (V.J.Cook) Soják in flooded conditions was dependent on stem height and the presence of photosynthetic material above the waterline. Completely submerged plants did not survive to the end of their four-week experiment.

Increases in salinity may restrict the ability of macrophytes to mitigate the effects of rising water levels. As salinity increases, rates of photosynthesis and biomass production typically decrease in non-halophytic macrophytes (Sculthorpe, 1985). Biomass allocation patterns can also shift as salinity increases, with lower proportional investment in above-ground tissues and increasing allocation of biomass to roots as changes in osmolarity restrict uptake of water and nutrients (Morris and Ganf, 2001). These responses to salinity are the opposite of what is required for some species to tolerate increases in water depth, particularly in cases where rapid height growth for maintenance of photosynthetic area above the waterline is a determinant of survival success (Rea and Ganf, 1994; Siebentritt and Ganf, 2000; Morris and Ganf, 2001). Consequently, increases in salinity may reduce tolerance to inundation and restrict the potential elevation ranges of susceptible species within salt-affected wetlands.

This study explored the potential effects of increases in salinity and water depth on the distributions of macrophyte species found in wetlands on the floodplain of the Clarence River, a coastal river located in northern New South Wales (NSW), Australia. Most oligohaline and mesohaline wetlands on the Clarence River floodplain have been affected by drainage and tidal exclusion due to flood mitigation infrastructure installed from the 1950s to 1980s (Pressey, 1989; Smith, 2011); over 140 drains were fitted with one-way tidal gates that increased drainage rates while preventing tidal exchange between floodplain wetlands and adjacent tidal waterways (Pressey and Middleton, 1982; Pressey, 1989; Williams and Watford, 1997). Drainage and tidal exclusion have caused the activation of acid sulphate soils at a number of sites, leading to surface scalding, reduced water quality and vegetation loss (Pressey and Middleton, 1982; Smith, 2011). One proposed remediation measure is the modification of flood gates to allow river water to flow back into these secondarily fresh wetlands during periods of low salinity (Pressey and Middleton, 1982; Walsh and Copeland, 2004).

In this paper we present the findings of an experiment conducted to determine if increases in salinity that are large enough to affect plant growth rates can reduce the functional depth tolerance ranges of low-growing and emergent macrophyte species. We used an outdoor tub experiment to test the effects of four levels of salinity, at three water depths, on the growth and survival of four low-growing or emergent macrophyte species, *B. caldwellii*, *Cynodon dactylon* (L.) Pers, *Eleocharis equisetina* C.Presl and *Paspalum distichum* L. Specifically, we tested: (1) how increases in water depth affected the growth and survival of each species; and (2) if exposure to increased salinity levels reduced the abilities of these species to survive increases in water depth.

2. Materials and methods

2.1. Plant material

We selected four species with distributions that could potentially be affected by changes in wetland salinity and inundation regimes. All species are common in secondarily fresh wetlands affected by drainage and floodgates (C. Johns, unpublished data). *Eleocharis equisetina* and *B. caldwellii* are emergent rhizomatous sedges that can form dense stands in areas of shallow water; *E. equisetina* has basal meristems and narrow (1–3 mm diameter) leafless cylindrical culms to around one metre height and *B. caldwellii* has culms to 1.2 m height with apical meristems and true leaves (*c.* 2–7 mm wide) (Wilson, 1993). *Paspalum distichum* and *C. dactylon* are low-growing stoloniferous grasses (Jacobs, 1993); *P. distichum* occurs on damp ground or in shallow water and can produce long, floating stems, sometimes forming floating mats; *C. dactylon* is a terrestrial species and often occurs immediately above the high waterline of these wetlands.

Approximately 250 plants of each species were collected from two wetlands on the Clarence River floodplain during August 2006. These were a freshwater area (29°25′09″S, 147°6′07″E) of the Broadwater wetland and a ponded freshwater section of Everlasting Swamp (29°31′23″S, 147°3′32″E). Plants were washed and trimmed to a standard size before potting. Individual tufts of *E. equisetina*, rhizomes of *B. caldwellii* and stolons of *C. dactylon* and *P. distichum* were established by potting into separate 2.8 L pots, filled with equal parts sand, peat and loam.

Pots were subsequently kept in trays of water, 10 cm deep, in an unheated polyhouse (day/night temperatures 35 °C/12 °C) with natural light. Pots were rotated regularly to minimise possible position effects on growth. After two months, 144 plants per species, of uniform size (median heights; *B. caldwellii* 119 cm, *C. dactylon* 43 cm, *E. equisetina* 28 cm and *P. distichum* 80 cm), were selected and randomly allocated to the experimental treatments.

2.2. Experimental design

Plants were subjected to three water depths (pot rims 5, 20 and 60 cm below the water surface) and four salinity concentrations (fresh, 2500, 5000 or 10 000 mg L^{-1}). The experiment was conducted outdoors in 16 round fibreglass tubs (110 cm diameter, 75 cm deep), with mean day/night temperatures 25 °C/12 °C and relative humidity 67%/44%. The tubs were arranged in four replicate blocks with one tub per block allocated randomly to each of the salinity treatments. Plastic platforms were used to position plants at each of the three depths in each tub, with one platform per depth. Pot positions were rotated every 7–10 days. In total, we subjected 12 plants per species to each of the 12 salinity × depth treatment combinations. At the start of the experiment all *B. caldwellii* plants were tall enough to exceed the waterline in all treatments, while some *P. distichum* plants and all *E. equisetina* and *C. dactylon* plants were completely submerged in the deepest treatment.

We achieved the salinity treatment concentrations of 2500, 5000 and 10 000 mg L^{-1} using a commercially available aquarium sea salt (Ocean Nature® sea salt, AQUASONIC, Wauchope, NSW) dissolved in tap water. Fresh water tubs contained tap water only (salinity *c.* 200 mg L^{-1}). Tubs were filled with fresh water as the plants were placed in position. Then we increased the salt concentrations by one third of the target concentration per day over three days. We monitored salt concentrations throughout the experiment, using a YSI™-30 hand-held temperature-compensated salinity meter (Xylem Inc., Eastern Creek, NSW), and maintained salinities (to within 200 mg L^{-1} of the treatment target) by topping the tubs up with fresh water every one to two days to compensate for evaporation. All plants were harvested after eight weeks. The experiment was ended at this time to avoid the potentially confounding effect of canopy overlap and competition for light on interpretation of the main treatment effects.