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REGULAR ARTICLE

The response of the mangrove *Avicennia marina* to heterogeneous salinity measured using a split-root approach

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Abstract
Aims To investigate the physiological processes underlying freshwater utilisation in halophytes under non-uniform salinity conditions in order to determine whether preferential uptake of freshwater occurs and whether transient freshwater availability improves plant water relations and photosynthesis
Methods In a split-root experiment, we grew *Avicennia marina* (Forssk.) Vierh. at uniform salinity conditions (35:35 ppt) and then lowered (35:5 ppt) or increased (35:65 ppt) salinity to one compartment. Using $\delta^{18}O$-labelled water we calculated the extent of preferential water uptake of either source.
Results When given a 35:5 treatment, *A. marina* took-up three times more water from the fresher compartment than predicted by a root-weighted-no-salinity-preference model. No difference between compartments was observed in the 35:65 treatment, suggesting that avoidance of the more saline water did not occur. In the 35:5 treatment, stomatal conductance increased within 1.5 h, but photosynthetic rates were not enhanced over the 48-h period of the experiment and rapidly decreased in the 35:65 treatment.
Conclusions *Avicennia marina* responds to transient freshwater patches by increasing water uptake from areas of the root zone where the salinity is better for growth. However, photosynthetic rates respond to the highest salinity in the root zone; thus, reductions in salinity in part of the root zone may enhance water storage in stem tissues but positive effects on photosynthesis may require longer periods.

Keywords Non-uniform salinity · Halophyte · Water relations · ^{18}O · Mangrove · Split root · Stem water storage

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Introduction

High salinity soils are often characterized by high levels of spatial and temporal heterogeneity in salinity (Silvestri et al. 2005). The ability of some halophytes to occupy high salinity soils is often linked to an ability to utilise less saline patches in the rhizosphere (Salzman and Parker 1985; Semeniuk 1983; Yakir and Yechielie 1995). Due to their location in the intertidal zone, mangroves are exposed to both terrestrial and marine water sources, which vary greatly in salinity ranging from 0 ppt to more than 160 ppt (160,000 mg L^{-1}) where evaporation is high (Ball 1998). The heterogeneity in

soil salinity within mangrove forests is therefore much greater than that experienced by terrestrial plants (Bazihizina et al. 2012) and varies both spatially (horizontally and vertically) and temporally (at various time scales).

The mangrove *Avicennia marina* may grow in coastal areas where soil salinity can exceed 90 ppt (Semeniuk 1983), but like all other plants, must exclude salt from their cytoplasm and maintain adequate water uptake where the soil water potential is low. Thus, despite tolerating high salinity environments, salinity negatively influences mangrove growth and productivity (Ball 1988). Optimal growth rates for *A. marina* are usually observed at relatively low salinity levels (10–20 ppt; Clough 1984), thus, in highly saline environments, pulses of low salinity water may be important for sustaining growth and productivity.

Avicennia marina can have multiple stems and can reach heights of more than 13 m (Saenger and Snedaker 1993) and tends to have a more expansive root system than other mangrove species (Comley and McGuinness 2005). With such a large below ground biomass, the roots of plants of *A. marina* are inevitably exposed to heterogeneous salinities throughout the rhizosphere. While salinity might be high in part of the rhizosphere, some roots may remain in contact with less saline water sources (e.g., groundwater, rainwater or riverine water). When these less saline water sources are available, they can become an important source of xylem stream water, as has been documented for some mangrove species (Ewe et al. 2007; Lambs et al. 2008; Lin and Sternberg 1992; Sternberg and Swart 1987; Wei et al. 2013), yet it remains unclear whether there is preferential uptake of freshwater or whether this is a reflection of the higher abundance of fresh water in the rhizosphere.

Despite the obvious advantage of having access to sources of fresh water, temporally transient reductions in salinity, or spatial heterogeneity within the rhizosphere have not always proven beneficial to plant growth when compared to plants existing in higher but more stable saline conditions. There are a number of hypotheses that have been suggested to explain the effect of heterogeneous salinities on plant productivity and growth with suggestions that productivity is affected by either 1) the most saline part of the root zone, 2) the least saline part of the root zone and 3) the mean salinity or root-weighted mean salinity of the soil (reviewed in Bazihizina et al. 2012). The effect of heterogeneous salinity on plant growth and productivity may be species specific. Pepper plants growing in split root systems with saline and non-saline compartments were observed to have CO_2 assimilation rates and stomatal conductance similar to those of plants receiving saline conditions on both compartments of the root system and both assimilation and stomatal conductance were much lower than plants receiving freshwater in both compartments (Lycoskoufis et al. 2005) supporting hypothesis #1. In cotton growing in a split-root experiment, plant biomass was determined by the lowest salinity in the root zone (Dong et al. 2010), supporting hypothesis #2. However, growth and photosynthesis of the halophyte *Artiplex nummularia* was determined by the mean salinity of the root zone (Bazihizina et al. 2009), supporting hypothesis #3.

Fluctuations in salinity can have a more negative effect on photosynthesis and growth than stable salinity regimes, even with the same or higher mean salinity, as has been shown for the mangrove *Rhizophora mangle* (Lin and Sternberg 1993). Surprisingly, halophytes can be quite unresponsive to short term changes in salinity. A microarray study on the mangrove *Ceriops tagal* revealed very few transcriptional changes during the first 24 h of salt stress, suggesting a limited short-term response to changes in salinity (Liang et al. 2012). Short term changes in salinity from 75 to 500 mol m^{-3} NaCl over a period of a few days and then a rapid return to low salinity concentrations did not affect photosynthetic rates in *Plantago maritima* and only had a minor impact on stomatal conductance on the fourth day of the treatment (Flanagan and Jefferies 1989).

Based on prior work of the differences in water sources used by mangrove species (e.g., Ewe et al. 2007) we expected that limitations to growth and productivity originating from osmotic limitations to water uptake should be alleviated when part of the root system has access to water sources with greater water potential. Mangroves maintain osmotic potentials lower than the porewater (Scholander et al. 1962), thus decreases in porewater salinity will create a strong gradient to drive water uptake, although aquaporins must also be open to permit high rates of water uptake (Reef and Lovelock 2014).

In this study we grew the mangrove *A. marina* in a split-root system (Shani et al. 1993; Wiersum 1958) in order to firstly measure whether *A. marina* rapidly responds to changes in salinity to only part of its root zone. Using isotopically labelled water we determined whether preferential uptake of the different water sources

offered to the seedlings occurred and we assessed how photosynthetic gas exchange is affected by short-term changes in salinity testing whether photosynthetic gas exchange was sensitive to the highest, lowest or mean salinity of the root zone.

Methods

Plant material and cultivation

Seventy *Avicennia marina* (Forssk.) Vierh. propagules were collected in July 2013 at Downey Park Hockey Fields, Brisbane (27°34′S 153°17′E) and placed in seedling trays filled with a sandy loam vermiculite mix and kept in a glasshouse exposed to natural sunlight and photoperiod at the University of Queensland, Brisbane, Australia. Following the emergence of roots (after approximately 2 weeks), the propagules were transplanted so that the root system was divided evenly between two adjacent $11 \times 11 \times 12$ cm^3 pots containing 60:40 top soil : sand mix. Seedlings received 150 ml of saline nutrient solution to the soil of each of the pots three times a week for 4 months. The pots were maintained at field capacity and had a perforated bottom so the solution flushed the pots and drained through the sandy soil limiting salt buildup over time. The saline nutrient solutions consisted of Ocean Nature Sea Salt (Aquasonic Pty Ltd, Wauchope, NSW, Australia) that unlike natural seawater does not contain dissolved phosphate or nitrogen, and a nutrient complement formulated to directly reflect the low nutrient environment of the mangrove forest comprised of 0.01 mM NH_4NO_3; 0.004 mM KNO_3; 0.00032 mM NaH_2PO_4 and 0.161 mM NaFeDTPA. The sea salts were added to the pre-prepared nutrient solution in batches of 200 L to make a seawater salinity solution of 35 ppt. To reduce salt build-up on the leaves and mimic natural rain events, seedlings were sprayed with a fine mist of tap water for 15 s once weekly.

Treatment application and harvest

On the 25th of November 2013, 50 similar sized seedlings were selected, and simultaneously received one of 3 salinity treatments. At the time of treatment application, seedling height ranged from 30 to 40 cm and seedlings had 3–5 leaf pairs and a root biomass of approx. 1 g. The cotyledons were no longer attached to the seedlings. The plants were not watered for 2 days prior to the treatment application. The treatment (150 ml to each compartment) was applied simultaneously to both compartments of the split root system (compartment A: compartment B): 35:35 ppt (control), 35:5 ppt and 35:65 ppt. In order to distinguish between the water from each compartment, we used ^{18}O labelled water for compartment-B treatments (Sigma 329878). Compartment A received a saline tap water solution with a $\delta^{18}O$ signature of −3.95 ‰ (±0.04 SD), while compartment B received a saline isotopically-enriched tap water solution with a $\delta^{18}O$ signature of 24.65 ‰ (±0.19 SD). Water percolated through the bottom of the pots within 1 min of treatment application in all samples but one, which was removed from further analyses. Prior to treatment application 5 seedlings were harvested. Five seedlings from each treatment were then harvested 1 h, 24 h and 48 h following the treatment application. During harvest, the stem was cut at the soil surface and the lower 10 cm segment of the stem (with leaves removed) was sealed in a vial and placed on ice for later analysis of isotopic composition of the water. The root systems from each compartment of the pots and the leaves from the stem were separated and sealed in bags, which were kept on ice until later analysis. The leaves from each of the seedlings were weighed and then dried at 60 °C for 4 days before being re-weighed. The difference in mass was used to calculate water content. Root biomass for each compartment was measured after washing the roots in freshwater and then drying them for 4 days at 60 °C. In one seedling, from the 35:65 treatment, the split did not produce a somewhat even distribution of biomass between the pots and it was removed from further analyses, the split in other seedlings produced biomass ratios between the compartments that ranged between 0.5 and 2 with a mean (±SD) of 1.1 (±0.4). Three days following treatment application soil samples were taken from each pot and dried for 1 week at 60 °C. The soil salinity was then measured by mixing 1 g soil and 5 ml distilled water and measuring the salinity of the soil solution with a refractometer.

Gas exchange

Immediately prior to the treatment application, measurements of stomatal conductance to water vapour (G_s) and net photosynthetic CO_2 assimilation rate (A) were done from 10:00 AM on the newest fully expanded leaf for 8 seedlings from each treatment using a Li-Cor 6400 portable photosynthesis system (Li-Cor Corp. Lincoln,

NE, USA) equiped with a 6400–40 leaf chamber and a 6400–02 red LED light source with leaf irradiance set at 1000 μmol m^{-2} s^{-1}. Ambient air was used as a reference and leaf temperature was set at 30 °C. Measurements were repeated on the same seedlings 0.5, 1, 2, 24 and 48 h following the treatment application. For the 48 h sample, only 4 seedlings from each treatment remained.

Isotopic analysis of water source

We measured the amount of ^{18}O labelled water in the stem of the seedlings in order to determine the relative contribution of water from each compartment of the split pot system to plant xylem water. During the harvests prior to treatment application (time 0) and at 1 and 24 h following the treatment application, the shoots of the five seedlings from each treatment were cut off at the base and the lower 10 cm long segment of stem was immediately sealed in a 15 ml conical centrifuge tube. Tubes were kept on ice until transport to the laboratory. Stems were later (~5 h) frozen and kept at −20 °C until further analysis. Stem water was extracted from each sample by cryogenic distillation using a vacuum system at the Biogeochemistry Centre at the University of Western Australia following the procedures of West et al. (2006). The water extracted from the twigs was analyzed for $\delta^{18}O$ and δ2H abundance on a Picarro Cavity Ring-Down Spectrometer L1115-I (Picarro, Sunnyvale, CA). δ values are reported relative to V-SMOW. Three water samples from each of the water sources (compartment A water and compartment B water) were analysed alongside the water extracted from the stems. Due to the small size of the stems, the distillation from a small number of samples failed.

Preference for ^{18}O labelled compartment-B water was measured relative to a 1:1 model, taking into account difference in root biomass within each compartment. Stem isotope data from control (35:35) plants was used to generate a linear regression model for 1:1 water uptake (where no preference for water from either compartment is expected) as a function of the root biomass difference between the compartments (Fig. 1). Using this model, values for expected uptake under a no preference (1:1) scenario were calculated. The ratio between the observed values of $\delta^{18}O$ stem concentration and the expected values under a 1:1 scenario was then calculated for each seedling.

The salinity treatment application flushed the pots to the extent that it resulted in a significant change in soil salinity (Fig. S1), significantly increasing salinity of the (^{18}O labelled) B compartment in the 35:65 treatment and significantly decreasing salinity of the B compartment in the 35:5 treatment.

Results

In order to determine whether preferential uptake of water from either compartment of the split root system occurs while taking into account differences in root biomass between both compartments, we modelled the relationship between stem water isotopic composition and the proportion of root biomass between the two compartments under conditions where no preferential uptake from either compartment is expected. We measured the $\delta^{18}O$ in stem water of the 35:35 plants, where no preferential uptake is expected from either compartment as a function of the proportion of root biomass

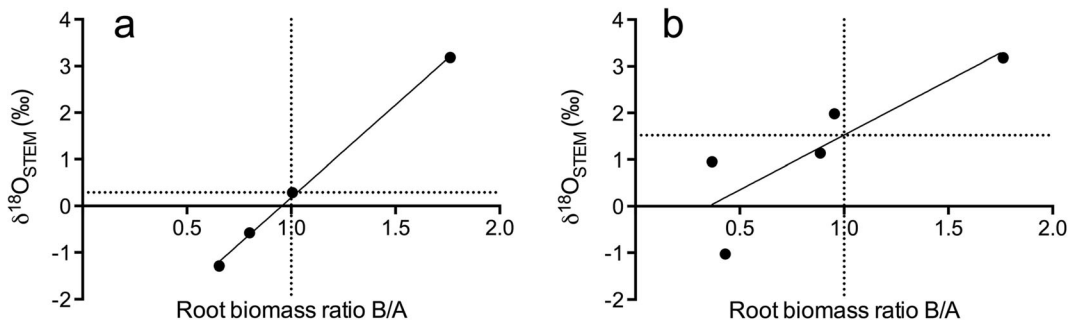

Fig. 1 Correlation between the $\delta^{18}O$ of stem water and the ratio between the root biomass in compartment B and compartment A for seedlings of *Avicennia marina* from the 35:35 treatment. Compartment A received tap water with a $\delta^{18}O$ signature of −3.95 (±0.04 SD), while compartment B received enriched tap water with a $\delta^{18}O$ signature of 24.65 (±0.19 SD). **a** 1 h following the treatment application, the regression was $\delta^{18}O$=3.98 (B/A ratio) - 3.82; R^2=0.99. **b** 24 h following the treatment application, the regression was $\delta^{18}O$=2.35 (B/A ratio) - 0.82; R^2=0.72

between the compartments. Isotopic composition was highly correlated with the amount of root biomass in each compartment (R^2=0.99, $\delta^{18}O$=3.98 (B/A ratio) - 3.82, 1 h after the treatment application (Fig. 1a); and R^2=0.72, $\delta^{18}O$=2.35 (B/A ratio) - 0.82, 24 h after the treatment application (Fig. 1b). The linear regression parameters were used to calculate the expected isotopic composition in seedlings from all treatments, assuming no preference for water uptake from either compartment. To assess the volume of the stem water that can be readily replaced (e.g., water within the xylem and phloem vs. water held in the pith), we used 1 h and 24 h data following the 35:35 treatment application. Under conditions of even root distribution between the two compartments, stem water $\delta^{18}O$ was 0.22‰ and 1.52‰, 1 h and 24 h following the treatment application (as indicated by dotted lines, Fig. 1a and b, respectively) while the modelled expected value if all stem water was made up recently acquired xylem water would be 10.35‰ (the mean value of the two water sources). Thus the turn over of the water pool made up approximately 2 % of the stem water volume 1 h after treatment and 15 % of the stem water volume 24 h after the treatment.

An analysis of the root weighted isotopic composition in stem water (Fig. 2a) revealed that water from both the A and B compartments was utilised. The root biomass allocation between the compartments is presented in Fig. 2b. The applied water did not significantly appear in the stem xylem during the first hour following application but by 24 h following the treatment application there were significant differences between the treatments in the preference of water from one compartment over the other (ANOVA, $F_{(2,10)}$=4.4, p=0.04, Fig. 2a). Compartment B (5 ppt) was significantly preferred over compartment A (35 ppt) in the 35:5 treatment, with a nearly threefold increase in uptake relative to a 1:1 model (Tukey HSD, p=0.04 relative to 35:35, Fig. 2a). When the salinity of compartment B was higher than compartment A (increased to 65 ppt), no significant effect was observed relative to the 35:35 treatment (p=0.96, Fig. 2a). The $\delta^{18}O$ values of the stem water can be found in Fig. S2.

In order to overcome the normal fluctuations in gas exchange over the course of the day, we normalised data for our analysis from 35:5 and 35:65 plants against the controls (35:35) at each time point. Error terms were derived using Taylor expansion for error propagation. The non-normalised gas exchange values can be found in Table S1. The gas exchange measurements indicate that the seedlings responded to the salinity changes in

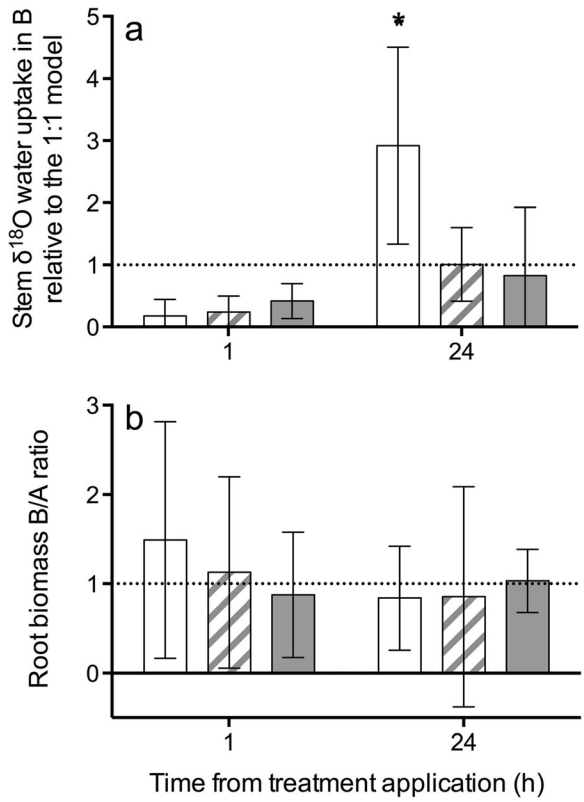

Fig. 2 Stem water $\delta^{18}O$ uptake from compartment B relative to compartment A of the split-root experiment. Compartment A salinity was always 35 ppt. Compartment B salinity was 5 ppt (*white bars*), 35 ppt (*thatched bars*), or 65 ppt (*grey bars*). Data is from stems collected 1 h and 24 h following the salinity treatments. **a** Stem water $\delta^{18}O$ in compartment B relative to a 1:1 model where no preference for either compartment is expected (dotted line). **b** Ratios between the root mass in compartment B and compartment A. Data are means±SD, N=4–5 plants for each bar. The asterisk indicates a significant departure from the 1:1 water uptake model

the compartments. Carbon assimilation rates (A) in plants receiving 65 ppt salinity in one of the compartments were significantly lower than in control (35:35) plants after 30 min of treatment application and remained significantly lower for an hour (ANOVA, $F_{(2,122)}$=6.1, p=0.003, Fig. 3a). There were no significant differences between treatments after 1.5 h, but A in 35:65 plants remained lower than control values throughout the experiment. Plants in the 35:5 treatments had carbon assimilation rates similar to control plants at all time points. Stomatal conductance was significantly higher in 35:5 plants relative to control 90 min following the treatment application (Fig. 3b).

The relative water content in leaves did not vary among treatments (ANOVA, $F_{(2,48)}$=0.27, p=0.77, Fig. 4), but it significantly increased within 1 h

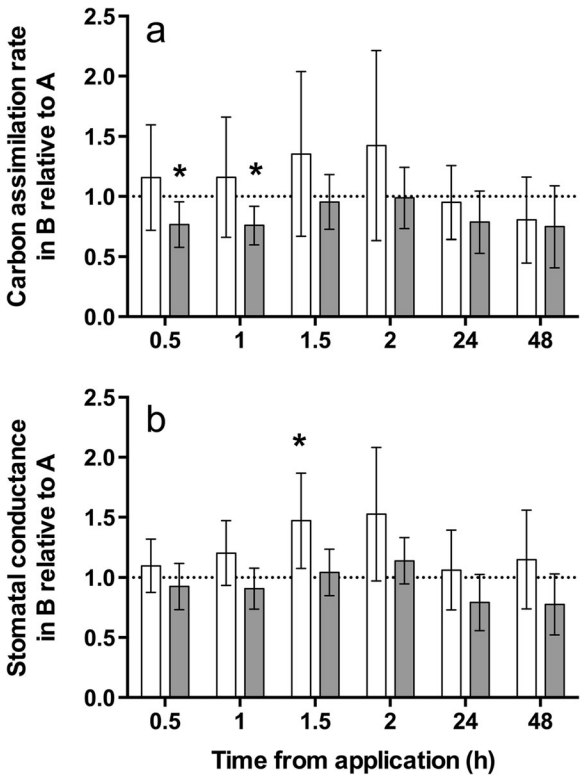

Fig. 3 Time series of gas exchange of the split root experiment in *Avicennia marina* seedlings as a proportion of the salinity treatment (*open bars*, 35:5; *grey bars*, 35:65 ppt) vs. the pretreatment application values (control, 35:35 ppt) relative to pre-treatment application. a) carbon assimilation rate and b) stomatal conductance. Error bars are 95 % confidence intervals around the mean. Values above the 1 (dotted line) in the ordinates indicate up regulation relative to control plants. N=7–8 for all bars, except for the 48 h data where N=3–4. Asterisks indicate a significant departure from control values

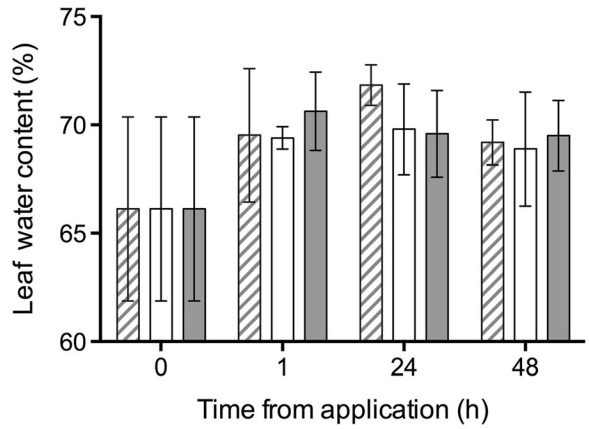

Fig. 4 Mean leaf water content per unit area of the split root experiment in *Avicennia marina* seedlings collected prior to (time 0, T_0) and after 1, 24 and 48 h following the treatment application. Treatment solutions applied were 35:5 ppt (white), 35:35 ppt to both compartments of the root system (control; thatched bars), or 35:65 (grey). Error bars are SD, N=8 for each bar except at 48 h, where N=4. Leaf water content in all treatments increased within 1 h of treatment delivery and remained significantly higher than T_0 for the next 48 h

following the treatment application regardless of the salinity treatment (ANOVA, $F_{(3,48)}$=7.4, p=0.0004; Tukey HSD p=0.0024) from 66.2 % (±4.2 % SD) in plants pre irrigation to 69.8 % (±2.1 %) and remained significantly higher for the next 48 h (Tukey HSD, p= 0.0003 and 0.0171 for the next 24 and 48 h respectively).

Discussion

When water with lower salinity was present in the rhizosphere, significant preferential uptake of the lower salinity water into the xylem stream occurred. A preferential uptake of freshwater has been demonstrated in a number of desert halophytes (Bazihizina et al. 2009; Yakir and Yechielie 1995), but not previously in mangroves. When higher salinity water was present, it contributed to xylem water in an amount proportionate to the root biomass in contact with that water, with no evidence of avoidance of higher salinity water. The fact that water uptake deviated from a 1:1 model only when the B compartment was fresher than the A compartment and not when it was saltier suggests an active process to enhance water uptake from the fresh water compartment rather than a simple physical phenomenon. Such an active process could be attributed to the opening of root water channels (Maurel and Chrispeels 2001). When exposed to heterogeneous water availability in the root zone, root hydraulic conductivity and aquaporin abundance have been shown to increase in roots exposed to higher water potentials (McLean et al. 2011). *Avicennia marina* maintains leaf water potentials that are at least 2 MPa lower than the water potential of the external solution (Downton 1982), thus water uptake from the high salinity compartment could still be achieved following the increase in salinity in the 35:65 treatment. Under 35:35 salinity conditions, a turnover of 2 % of the stem water occurred within 1 h following treatment application. In seedlings of *A. marina* growing under similar salinity conditions, xylem vessel lumen area makes up ~3 % of the stem area (Nguyen et al. 2015; Reef et al. 2012), thus it is likely that the rapid change in isotopic composition of the stem water represents the

turnover of the xylem pool. However, 24 h following the treatment application a turnover of 15 % of stem water occurred, indicating that within this time frame, assimilation of isotopically enriched water into other tissue types such as parenchyma had occurred, which could suggest water storage. The increase in relative water content in the leaves following the treatment application further suggests an increase in the internal water pool. Stem water storage can buffer the impacts of a heterogeneous environment varying in water availability or salinity by buffering transitional leaf water loss (Scholz et al. 2008). In an analysis of 37 tropical trees, stem water storage capacity was found to be strongly correlated to the ability of a species to grow (and flower) during the dry season (Borchert 1994). *Avicennia marina* can hold a considerable amount of water in secondary phloem and other tissues throughout the stem (Robert et al. 2014b) and has successive cambia with ample parenchyma tissues, which is proposed to be an adaptation in a range of species growing in water limited environments (Robert et al. 2014a). The relative increase in fresh water use in seedlings from the 35:5 treatment relative to control plants could be the result of increased water storage when less saline sources become available. The timing for refilling water storage tissue is intricately linked to environmental conditions in tropical trees (Goldstein et al. 1998). An observed rapid expansion of stem diameter following rainfall events in *A. marina* (Santini et al. 2015) supports the possibility of increased water uptake for storage purposes when less saline sources are available.

There are a number of hypotheses as to the effect of heterogeneous salinities on plant productivity and growth with suggestions that productivity is affected by either 1) the most saline part of the root zone, 2) the least saline part of the root zone and 3) the mean salinity or root-weighted mean salinity of the soil (reviewed in Bazihizina et al. 2012). In our experiment, photosynthesis rates increased slightly with the split-root reduction in salinity, but this increase was not significant. Photosynthesis responded to the highest salinity (supporting hypothesis 1), not to the mean salinity of the root zone, as shown by the similar photosynthetic rates between the 35:35 control plants and the 35:5 plants, which despite preferentially taking up water from the fresher compartment, did not enhance photosynthetic rates over the short term. Photosynthetic rates in the 35:65 plants were significantly lower than the 35:35 control plants, despite sharing a similar lowest salinity. A similar response was observed for pepper plants, where salinisation of only half the root system had a similar effect to the salinisation of the entire root zone (Lycoskoufis et al. 2005) and grapevines, where the adverse effects of salinity were not overcome even if part of the root system was exposed to fresh water and the fresh water preferentially taken up (Shani et al. 1993).

When fresher water became available, stomatal conductance significantly increased, albeit slightly, corroborating previous studies of significant increases in water uptake following a sudden lowering of salinity to part of the root zone (e.g., following a rainfall event, Santini et al. 2015). But despite the higher stomatal conductance, carbon assimilation did not significantly increase. This is similar to the response of the mangrove *Rhizophora mangle* to salinity fluctuations, which had similar and even lower photosynthetic rates than when grown at a constant salinity treatment, even if the constant salinity was higher than the mean of the fluctuation (Lin and Sternberg 1993). Many of the adaptations of halophytes such those of *A. marina* to salinity are not plastic on short temporal scales (Reef and Lovelock 2014), thus it is unclear whether *A. marina* can capitalise on short-term reductions in salinity to part of the root zone. For example, gas exchange is ultimately controlled by leaf anatomy and stem hydraulic conductance (Sperry et al. 1998; Terashima et al. 2011) so it might not be possible to respond to transient changes in salinity if the anatomy of the xylem already places strong limitations on water transport or if other non-stomatal limitations to photosynthesis occur. Non-stomatal limitations to photosynthesis, which could have developed due to the long term growth at higher than optimal salinity, e.g., due to low mesophyll conductance, lower rates of PSII photochemistry or lower concentrations of RUBISCO, cannot be altered on such short time frames (Delfine et al. 1999). Thus, short rainfall events or other events that alter the salinity in small parts of the root zone may not have a significant immediate overall effect on mangrove productivity, despite a significant uptake of the lower salinity water.

We show here that over short time periods the photosynthetic rates of *Avicennia marina* respond to the highest salinity in the root zone. Thus, a short term lowering of salinity to part of the root zone (e.g., a rainfall event) is unlikely to provide an immediate benefit to mangrove productivity when compared to longer, less transient, changes in salinity. However, the preferential uptake of fresher water when it occurs may still

have a positive impact on growth rates by reducing the need for the production of energetically costly osmotically active metabolites (Raven 1985) thus freeing more resources towards growth. Furthermore, stems of *A. marina* have a capacity for considerable water storage (Vandegehuchte et al. 2014), therefore the ability to preferentially take up of fresh water when it becomes available could support future photosynthetic carbon gains in this species and water storage in *A. marina* can be important during periods of physiological drought. The size of the xylem water pool was 2 % of the stem water volume (Fig. 1a), similar to prior estimates (Nguyen et al. 2015; Reef et al. 2012), thus most of the water in the stem is contained within tissues other than the xylem (e.g., pith and secondary phloem, Robert et al. 2014b). Our experimental study has shown that *A. marina* seedlings growing under soils with heterogeneous salinities had a preferential uptake of fresh water sources. Fresh water sources enhanced stomatal conductance, however photosynthetic rates were determined by the highest salinity in the root zone even when fresh water sources were available. Our findings of a high capacity for water storage within stems may be associated with the successive cambia trait that could be important in tolerance of habitats with low water availability or high salinity. Water storage may be an important mechanism to maintain metabolic functioning in *A. marina* when exposed to high salinity soils (i.e., during droughts) but may also be a short-term response that may not enhance growth rates and productivity in mangrove trees in the short term.

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Compliance with Ethical Standards The authors declare that they have no conflict of interest. All authors have contributed to this work and have consented to this submission.

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