PRIMARY RESEARCH PAPER

The use of fresh and saline water sources by the mangrove *Avicennia marina*

**Nadia S. Santini · Ruth Reef ·
David A. Lockington · Catherine E. Lovelock**

Abstract Mangroves are distributed along tropical and subtropical riverine and coastal shores. Although mangroves are highly adapted to saline environments, maintaining water uptake under saline conditions is energetically expensive. Therefore, salinity is a limiting factor for mangrove growth and productivity, and access to fresh water sources, such as rainwater and groundwater, which reduce water salinity, increase mangrove ecosystem productivity. Here, we investigated the extent of fresh water utilization by mangroves to better predict current and future mangrove productivity. We used the abundance of ^{18}O isotope in stem water to assess: (1) the extent of fresh water utilization by *Avicennia marina* (Forssk.) Vierh across hydrological settings; and (2) whether growth, measured as increments in stem circumference, is sensitive to variation in rainfall availability. The δ^{18}O isotopic composition of stem water indicated mangroves use both fresh and saline water sources for metabolic processes. However, our results suggest that the proportion of fresh water used by mangroves increases with the availability of fresh water. Growth of the main stems of trees was correlated with rainfall ($r^2 = 0.34$ and $r^2 = 0.37$, $P = 0.001$). Our results indicate that access to fresh water is important for mangrove productivity because it enhances their growth rates.

Keywords Isotopes · Salinity · Exmouth Gulf · Queensland

N. S. Santini · R. Reef · C. E. Lovelock
The School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

N. S. Santini (✉) · D. A. Lockington · C. E. Lovelock
The National Centre for Groundwater Research and Training, Flinders University, Adelaide, SA 5001, Australia
e-mail: nadiasilvanasantini@gmail.com

D. A. Lockington
The School of Civil Engineering, The University of Queensland, St Lucia, QLD 4072, Australia

Introduction

Mangrove forests inhabit the coastal and riverine shores of the tropics and sub-tropics (Alongi, 2009). Due to their position in the intertidal zone, mangroves can access water from a range of different sources. Soil pore-water can be composed of rainwater, groundwater and tidal water from the adjoining rivers, creeks or sea. The salinity of the pore-water surrounding the roots of mangroves varies with rainfall, evaporation (and transpiration), and frequency of tidal inundation (Upkong, 1991). Low in the intertidal zone,

mangrove soils are regularly inundated and subject to relatively constant salinity with values similar to the salinity of the water in the adjoining creek or sea. Higher in the intertidal, where soils are less frequently inundated, pore-water salinities fluctuate depending on rainfall, groundwater and evaporation. In arid environments, pore-water salinity can become hypersaline due to high levels of evaporation. However, where groundwater enters the mangroves, or during periods of high rainfall, pore-water salinity can be reduced (Semeniuk, 1983; Susilo et al., 2005; Alongi & Brinkman, 2011). Shallow groundwater enters mangroves via seepage of water moving from hinterlands into tidal mangrove lands (Semeniuk, 1983; Lambs et al., 2008). Surface and subsurface seepage often originates from rainfall and finds preferential pathways through the porous substrates, invading the groundwater tidal systems that may otherwise be hypersaline (Lambs et al., 2008; Humphreys et al., 2009).

Mangroves are adapted to highly saline environments. Mangroves can exclude up to 97% of the salt in the soil pore-water from entering the xylem stream (Ball, 1988) and use salt ions for osmoregulation and for maintaining sufficiently low tissue water potentials for water uptake (Scholander, 1968). Due to the energetic costs associated with maintaining water uptake under saline conditions, soil salinity has long been recognized as an important factor that limits mangrove growth and productivity (Ball, 1988; Lovelock et al., 2006).

The widespread mangrove species *Avicennia marina* can tolerate salinities up to 90 ppt (Hutchings & Saenger, 1987); however, the optimum salinity levels for *A. marina*'s growth range from 3.5 to 17.5 ppt (Clough, 1984; Ball, 1988). Growth declines linearly with increasing salinity (Morrisey et al., 2010). Therefore, mangroves growing at salinities higher than those optimal for growth benefit from periodic increases in fresh water availability. This is why tree growth (Menezes et al., 2003) and the diversity and abundance of mangroves (e.g. Smith & Duke, 1987; Eslami-Andargoli et al., 2009) have been found to increase with increasing rainfall.

It is possible to determine the use of different water sources by mangroves by investigating the abundance of natural stable isotopes of oxygen (O) within their tissues. The abundances of ^{18}O and ^{16}O isotopes can vary greatly between water sources. Because no

evidence for oxygen fractionation has been observed during water uptake in plants (Lin & Sternberg, 1993; Ellsworth & Williams, 2007, in contrast to hydrogen), the $^{18}O/^{16}O$ ratio ($\delta^{18}O$) of the stem water reflects the $\delta^{18}O$ of the water sources taken up by the plant.

There have been three previous studies of the use of different water sources by mangroves conducted in the Everglades in Florida, where the wetland system is underlain by highly permeable limestone (Sternberg & Swart, 1987; Lin & Sternberg, 1992; Ewe et al., 2007); one study in French Guiana where sand banks separate the mangroves from the freshwater marshes (Lambs et al., 2008) and one in an estuarine setting in Australia (Wei et al., 2012). These studies indicate that water sources available to mangroves vary over landscapes (Sternberg & Swart, 1987; Lambs et al., 2008; Wei et al., 2012). They also indicate that the water sources used by mangroves at any location vary over seasons, with rainfall preferentially used during wet seasons (Lin & Sternberg, 1992; Ewe et al., 2007; Wei et al., 2012). While the use of varying water sources may directly reflect the availability of different water sources (Sternberg and Swart, 1987; Lambs et al., 2008), it appears that the water sources used by mangroves can vary within similar habitats. For example, in Florida, the $\delta^{18}O$ of stem water from *Rhizophora mangle* trees in the fringing forest (which is frequently inundated by tides) was similar to values typical of seawater in both the wet and the dry seasons (Lin & Sternberg, 1992), while in Australia fringing *Avicennia marina* mangroves used a mix of fresh and saline water sources during both seasons (Wei et al., 2012).

Here, we assessed the extent of fresh water utilization by mangroves by studying $\delta^{18}O$ in stem water in a widespread species, *A. marina* over sites in varying hydrological settings: two inner estuarine sites with high levels of fresh water inputs, one outer estuarine site and two tidal creek sites which had strong marine influence. These sites had varying availability of fresh water inputs.

Materials and methods

Study sites

In this study, we used five sites from three locations with varying hydrological settings. Two of the sites
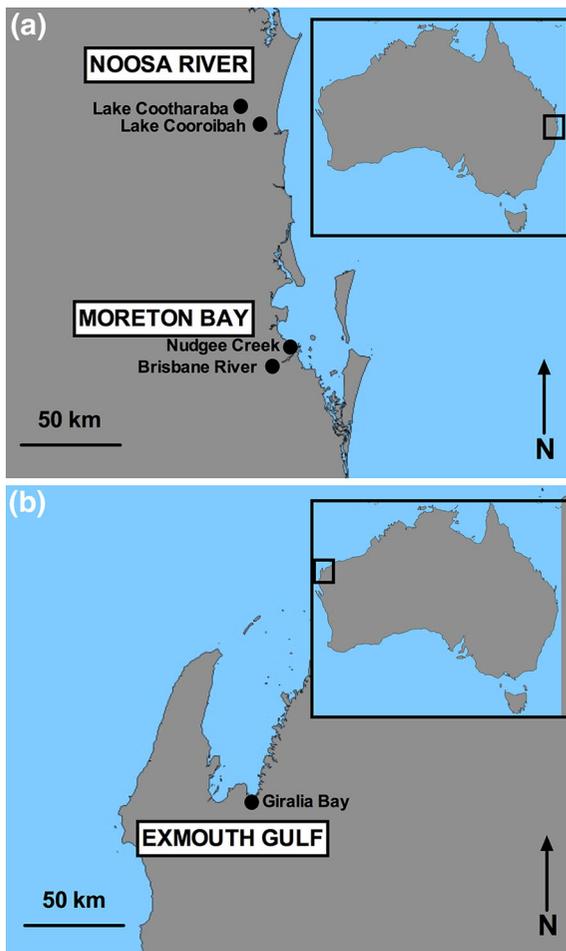
Fig. 1 Our study sites were located across hydrological settings. Two sites were within an inner estuarine setting: Lake Cootharaba and the Brisbane River. One site was in an outer estuarine setting: Lake Cooroibah, and two sites were in a tidal creek setting: Nudgee Creek and Giralia Bay

were located in an inner estuarine setting, Lake Cootharaba along the Noosa River and the Brisbane River in Moreton Bay, Queensland. One site was located in an outer estuarine setting, the Lake Cooroibah in the Noosa River, and two sites were located in a tidal creek setting, Nudgee Creek in Moreton Bay, and Giralia Bay, at the Exmouth Gulf, Western Australia (Fig. 1a, b).

Moreton Bay is a large semi-open bay that extends 90 km from north to south. The bay is well flushed through three passages to the open ocean and is also influenced by five rivers that drain into the bay (Dennison & Abal, 1999). Mangrove forests are well

developed on the western side of the bay. One site was within the mangrove forest that fringes Nudgee Creek, a tidal creek setting, within the Boondall Wetlands Reserve, 3 km inland from the coast (27.35°S, 153.08°E). Our second site in Moreton Bay is a forest in an inner estuarine setting fringing the Brisbane River, at The University of Queensland, 25 km from the mouth of the Brisbane River (27.50°S, 153.02°E). The climate is subtropical with a mean minimum temperature of 16°C, a mean maximum temperature of 25°C and a mean annual rainfall of 1,016 mm year^{-1}. Tidal range at the site is *ca.* 1.5 m (Australian Bureau of Meteorology, 2014).

Two other sites in Queensland that span a salinity gradient were located along the Noosa River, approximately 120 km north of the Moreton Bay study area. The Noosa River is an estuarine system characterized by a sand bar in the mouth of the river, which restricts seawater exchange (Hewson et al., 2001). The Noosa River is composed of shallow embayments and lakes (mean depth *ca.* 1 m) connected by a deeper river channel. One of our sites was in Lake Cooroibah (26.36°S, 153.04°E), an outer estuarine setting, 8 km away from the river mouth. The other, less saline site, was situated at Lake Cootharaba (26.31°S, 152.98°E), an inner estuarine setting, 19 km away from the river mouth. The mean annual rainfall is 1,628 mm year^{-1}. The mean minimum temperature in Noosa is 17°C and the mean maximum temperature is 25°C. Tidal range is *ca.* 1.2 m (Australian Bureau of Meteorology, 2014).

Our fifth site is located in Giralia Bay in the Exmouth Gulf, Western Australia (22.53°S, 114.3°E). The Exmouth Gulf is a large, open, inverse estuary with infrequent river flows that occur during cyclones (Brunskill et al., 2001). The study site was on the edge of a tidal creek within Giralia Bay. The climate in this region is arid and warm, with a mean annual rainfall of 230 mm year^{-1}. The mean minimum temperature in the region is 18°C and the mean maximum temperature is 32°C with peaks of 45°C in summer. Tidal range is *ca.* 1.3 m (Australian Bureau of Meteorology, 2014).

Sample collection

In the Moreton Bay sites (i.e., Brisbane River and Nudgee Creek) and in the Noosa River sites (i.e., Lake Cootharaba and Lake Cooroibah), we sampled plants
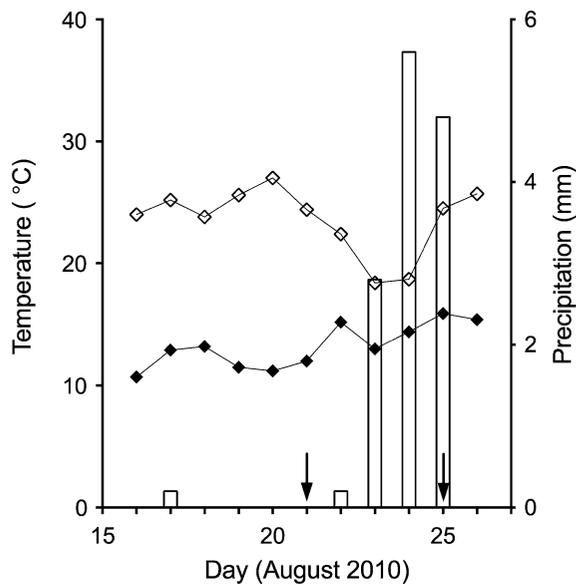
Fig. 2 Mean daily minimum (*filled diamonds*) and maximum temperature (*open diamonds*) and rainfall (*bars*) during the collection period at Giralia Bay in the Exmouth Gulf, Western Australia. Dates of stem water collection are marked with arrows. During the previous months (May, June and July) rainfall events were rare, with rainfall only during May and June. Rainfall occurred on May 19 (0.4 mm), May 23 (3.2 mm), June 4–7 (50 mm), June 15 (0.2 mm), June 16 (95 mm) and June 17 (0.2 mm). Data were obtained from the Australian Bureau of Meteorology (2014)

and water sources during March–April 2010. At Giralia Bay, we sampled during a dry period and then we re-sampled after a 3-day period of rain (21-Aug-2010 and 25-Aug-2010; Fig. 2).

To establish the $\delta^{18}O$ isotopic composition of water used by *A. marina*, we sampled fine, terminal branches from 3–10 fringing mangrove trees at each site. The terminal branches were 150 mm long with stem diameters of *ca.* 8 mm. Immediately following collection, the branches were sealed with Parafilm M (SPI Supplies, PA USA), put in collection tubes and kept at −20°C until further analyses.

Simultaneously with the collection of branches, we collected water from the different water sources ($n = 3$–10) at each site in 10 mL vials: mangrove soil pore-water, seawater, rainwater (which we sampled using vials within a rack container during the rainy periods) and tidal water (river water or creek water). Vials were completely filled in with water and sealed with Parafilm after collection to avoid evaporation. Soil pore-water was collected at 30 cm depth

where small roots, <20 mm diameter which comprises more than 50% of root biomass, are abundant (Komiyama et al., 1987). Pore-water was collected using a hand held suction device (McKee et al., 1988). In the Exmouth Gulf, we also sampled groundwater from the Giralia Pastoral Station homestead bores (−22.75°S, 114.39°E) which were 25 km away from the study site. We were unable to sample groundwater at the Queensland sites. Instead, we used values obtained from comparable estuarine sites in the region. For the Brisbane River and Nudgee Creek sites, Wei et al. (2012) provided values from the Tinchi Tamba Wetlands Reserve located within 15 km of our Moreton Bay sites. For the Noosa River sites, we used data from the literature from the Buttha and Poona coastal aquifers that are located within 24 km south and 50 km north from our Noosa River sites (Larsen & Cox, 2011). All the isotopic values of groundwater for our study correspond to shallow groundwater, which are those from aquifers of unconsolidated coastal deposits.

Water samples were extracted by cryogenic distillation using a vacuum system at the Stable Isotope Laboratory at the University of Western Australia following the procedures of West et al. (2006). Water samples were analysed for $\delta^{18}O$ abundance and results were normalized with the international standards provided by the International Atomic Energy Agency (IAEA): Vienna Standard Mean Ocean Water (VSMOW), Standard Light Antarctic Precipitation 2 (SLAP2) and Greenland Ice Sheet Precipitation (GISP). Salinity of the different water sources was measured using a Refractometer W/ATC 300011, SPER Scientific (Scottsdale, AZ, USA).

Stem growth

We monitored daily increments in circumference of the main stems of ten *A. marina* trees for 2 months (November-December 2010) at the sites along the Noosa River and in Moreton Bay, using electronic dendrometer bands (ICT International, Australia) (Lagergren & Lindroth, 2004). We recorded the increment in stem circumference of trees of *ca.* 30 cm circumference. To assess the sensitivity of stem circumference increments to rainfall, we obtained daily rainfall records from the meteorological stations that were closest to our sites: Brisbane Aero (station 40842), 3 km away from the Brisbane

Table 1 $\delta^{18}O$ isotopes from different water sources in our study sites

Site	Rainwater	Pore-Water	Seawater	Groundwater	Groundwater Reference	*A. marina* mangroves
Inner estuarine						
Lake Cootharaba	-1.86 ± 0.59[a]	-0.70 ± 0.09[ab]	0.96 ± 0.13[b]	-4.4 ± 0.44	Larsen & Cox (2011)	-2.27 ± 0.10[a]
Brisbane River	-4.12 ± 1.50[a]	-1.68 ± 0.11[ab]	0.70 ± 0.07[b]	-1.2 ± 0.20	Wei et al. (2012)	-2.73 ± 0.25[ab]
Outer estuarine						
Lake Cooroibah	-1.86 ± 0.59[a]	-0.29 ± 0.009[ab]	0.96 ± 0.13[b]	-4.4 ± 0.44	Larsen & Cox (2011)	-1.80 ± 0.15[a]
Tidal creek						
Nudgee Creek	-4.12 ± 1.50[a]	0.22 ± 0.002[ab]	0.70 ± 0.07[b]	-1.2 ± 0.20	Wei et al. (2012)	-1.28 ± 0.14[a]
Giralia Bay	-9.42 ± 0.07[a]	2.10 ± 0.05[b]	1.29 ± 0.19[b]	-6.43 ± 0.06[a]	Field	-1.28 ± 0.17[b]

Values are means $\pm$ standard errors and are expressed in ‰. Different letters along each row indicate that $\delta^{18}O$ values were significantly different among sources within sites. Values for groundwater at the Brisbane River and Nudgee Creek were obtained from the Tinchi Tamba Wetlands Reserve (Wei et al., 2012). Values for groundwater data for Lake Cootharaba and Lake Cooroibah were obtained from the Buttha and Poona coastal aquifers (Larsen and Cox, 2011). These values were not included in the statistical tests

River site and 6 km away from the Nudgee Creek site and Noosaville (station 40995), 5 km away from the Corooibah Lake and 12 km away from the Cootharaba Lake (Australian Bureau of Meteorology, 2014).

Data analyses

To assess the variation in $\delta^{18}O$ among water sources at each site, we performed a Kruskal–Wallis one-way analysis of variance (ANOVA) followed by a Dunn's post-test. We used the package SIAR from the software R (R Development Core Team, 2008) that uses a Bayesian model based on Gaussian likelihood to determine which sources of water mangroves use (Parnell et al., 2010). Seawater, rainwater, mangrove pore-water and groundwater were considered as water sources for the model. In Giralia Bay, in samples taken before a rainfall event, rainwater was not considered in the model as rainfall events were rare before the sampling campaign (there was only one rainfall event of 0.2 mm 4 days before sampling and no other rainfall event before the 17th of June, see Fig. 2). Tidal water was not included in the model to avoid duplication of water sources because the $\delta^{18}O$ signature of the tidal water was the same to that of the mangrove pore-water ($r^2 = 0.99$, $P < 0.05$). We evaluated the response of mangrove stem circumference increment to the amount of daily rainfall using linear regression analyses with the software R (R Development Core Team, 2008). Rainfall was log transformed prior to analysis to normalize the variance of the data.

Results

The isotopic signature of stem water across sites was depleted in ^{18}O, and values were lower in the inner estuarine sites (-2.73 ± 0.25‰ and -2.27 ± 0.10‰) than in the outer estuarine (-1.80 ± 0.15‰) and tidal creek sites (-1.28 ± 0.14 and -1.28 ± 0.17‰) (Table 1). These $\delta^{18}O$ values of the stem water were similar to more than one of the available water sources, indicating that *A. marina* uses a mixture of water sources for metabolic processes across hydrological settings.

To evaluate the proportional use of different water sources for metabolic processes by *A. marina*, we used the SIAR model that calculates confidence intervals based on posterior distributions using a Bayesian approach (Parnell et al., 2010). The posterior distributions of rainwater and groundwater across sites exhibited highly negative correlation coefficients, in the inner estuarine sites: -0.47 in the Lake Cootharaba and -0.67 in the Brisbane River, in the outer estuarine site: -0.52 and in the tidal creek sites: -0.43 in the Nudgee Creek and -0.89 in Giralia Bay. These negative correlation coefficients between rainwater and groundwater indicated that the model could not

differentiate between the two sources of water and that either rainwater or groundwater was used by *A. marina*. In addition, highly negative correlation coefficients were observed between mangrove pore-water and seawater in the outer estuarine site (−0.65) and in the tidal creek sites (Nudgee Creek, −0.75 and Giralia Bay, −0.90), indicating that pore-water and seawater were indistinguishable.

Because it was not possible to differentiate between rainwater and groundwater across sites, we grouped water sources as fresh water (rainwater and groundwater) for all the sites across hydrological settings. In addition, saline water sources (soil pore-water and seawater) were grouped at the outer estuarine site (Lake Cooroibah) and at the tidal creek sites (Nudgee Creek and Giralia Bay).

In the inner estuarine sites, *A. marina* used higher amounts of fresh water (21–43% at Lake Cootharaba and 29–46% at the Brisbane River) than in the outer estuarine site (13–20%) and those in the tidal creek sites (9–18% in the Nudgee Creek and 25–32% at Giralia Bay). Additionally, in the inner estuarine sites, *A. marina* used less saline water sources than in the outer estuarine site and in the tidal creek sites (Table 2).

During the dry period, in the tidal creek site of Giralia Bay, Western Australia, approximately a third of *A. marina*'s water use relied on groundwater sources (25–32%). At this site, we were able to test whether water use was altered by a rainfall event. We found that values of $\delta^{18}O$ in mangrove tissues were significantly more depleted in ^{18}O after rain (Fig. 3). The SIAR model indicated an increase in fresh water use of between 33–43% after the rainfall event.
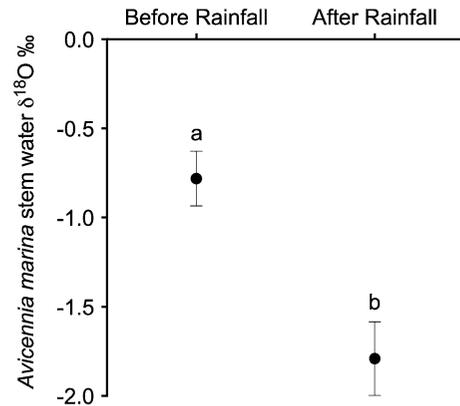

Fig. 3 $\delta^{18}O$ of *Avicennia marina* mangroves from Giralia Bay, Western Australia before and after a rainfall event. Values are mean and standard errors. The $\delta^{18}O$ means were significantly different as indicated by *different letters* ($P = 0.006$, $t = 3.57$, n total = 20)

Characterisation of salinity and ^{18}O isotopes of pore-water across our sites found that saline waters were frequently more enriched in the heavier isotope ^{18}O. Overall, the relationship between $\delta^{18}O$ and salinity of the water sources was positive but the slope varied significantly among our three major locations (Fig. 4). Mangrove pore-water exhibited higher $\delta^{18}O$ values in the outer estuarine and tidal creek settings compared to the inner estuarine sites (Fig. 4).

Consistent with the high level of fresh water used by trees indicated by our SIAR analysis of $\delta^{18}O$, we found that the relationship between rainfall and stem growth was significant in the Moreton Bay and in the Noosa River sites (Fig. 5). The slope of the regression between stem growth and rainfall was significantly

Site	Pore-water salinity (ppt)	Fresh water	Saline water pore-water (PW)/ seawater (SW)
Inner estuarine			
Lake Cootharaba	15 ± 0.6	21–43	PW 31–58/SW 11–58
Brisbane River	20 ± 1.2	29–46	PW 3–55/SW 8–53
Outer estuarine			
Lake Cooroibah	36 ± 1.0	13–20	64–87
Tidal Creek			
Nudgee Creek	34 ± 2.6	9–18	75–90
Giralia Bay-Before Rain	54 ± 0.9	25–32	68–75
Giralia Bay-After Rain	–	33–43	57–67

Table 2 Salinity of mangrove pore-water (means ± standard errors, $n = 3–4$) and proportion of different water sources used by *Avicennia marina* mangroves in our study sites

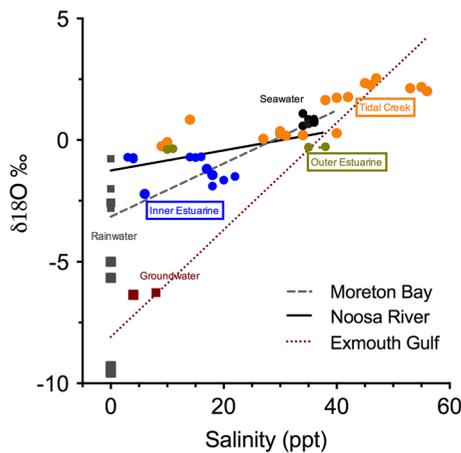Values are 10–90% percentiles as calculated by SIAR (Parnell et al., 2010)

Fig. 4 Relationship between $\delta^{18}O$ and salinity of water sources for three study regions. The lines are lines of best fit for each location. Between locations the slopes of the regression lines were significantly different ($P < 0.05$). For Moreton Bay, the regression is: $\delta^{18}O = 0.11$ Salinity—3.04 ($r^2 = 0.61$, $P = 0.0009$, $n = 14$). For the Noosa River the regression is: $\delta^{18}O = 0.04$ Salinity—1.30 ($r^2 = 0.53$, $P = 0.0005$, $n = 12$). For the Exmouth Gulf the regression is: $\delta^{18}O = 0.22$ Salinity—8.10 ($r^2 = 0.93$, $P < 0.0001$, $n = 15$). Different coloured symbols represent different water sources and hydrological settings: seawater (*black circles*), pore-water and river water from the inner estuarine settings (*blue circles*), pore-water and river water from the outer estuarine setting (*green circles*), pore-water and creek water from the tidal creek settings (*orange circles*), rainwater across hydrological settings (*grey squares*) and groundwater from the tidal creek site of Giralia Bay (*red squares*)

Fig. 5 Relationship between daily stem circumference increment and Log (Rainfall [mm] + 1). The slopes of the relationships for the Moreton Bay and Noosa River study areas were significantly different ($P < 0.05$). For Moreton Bay, the regression is: Increment = 34 Log (Rainfall [mm] + 1) − 10.5 ($r^2 = 0.34$, $P = 0.001$, $n = 244$) and for the Noosa River, the regression is: Increment = 62 Log (Rainfall [mm] + 1) − 20 ($r^2 = 0.37$, $P = 0.001$, $n = 366$)

different between locations but trees at all sites responded to increasing rainfall in a consistently positive way. Stem growth varied, but was mostly zero or slightly negative with zero rainfall (Fig. 5).

Discussion

The $\delta^{18}O$ values for *A. marina* and the SIAR models indicated that *A. marina* mangroves use fresh water sources for growth. However, our results suggest that the proportion of fresh water used by mangroves increases with the availability of fresh water. For example, mangroves from the inner estuarine sites used more fresh water than mangroves from the tidal creek sites (Table 1; Table 2). In the tidal creek setting of Giralia Bay, where rainfall events are scarce the stem water of *A. marina* mangroves was depleted in ^{18}O, which suggests that even during dry periods *A.*
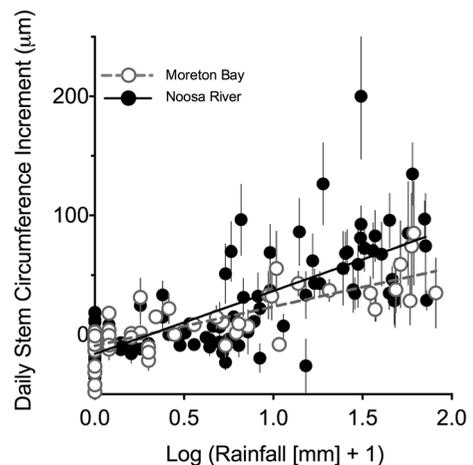
marina uses a proportion of fresh water for metabolic processes (Table 2). Our results suggest that mangroves have a flexible water-use strategy that uses both saline water and fresh water if available to maintain both growth and tissue salt balance in saline environments (Ball, 1988; Ye et al., 2005). In mangroves, hypersaline water increases energetic costs associated with water uptake and therefore limits growth and productivity (Ball, 1988; Lovelock et al., 2006). However, mangroves grow in saline environments and often rely on salt ions to assist with osmoregulation (Scholander, 1968).

At the tidal creek site of Giralia Bay, the $\delta^{18}O$ of *A. marina* stem water varied significantly before and after a rainfall event. This difference in $\delta^{18}O$ values indicated that *A. marina* is able to utilize water delivered in rainfall events. However, the isotopic signature of the stem water was significantly higher than the rainfall signature (Table 1, $P = 0.007$), indicating that *A. marina* used pore-water simultaneously with water delivered in recent rainfall. Mangrove root distributions and the association of roots with soil macropores, e.g. crab burrows (Stieglitz et al., 2013) and old root channels (McKee, 2001), where rainfall, tidal water and groundwater infiltrate the soils, may be features of mangrove root systems

that enhance access to intermittently available water sources (i.e. surface water, soil pore-water, ground-water) as well as to nutrients. Variation in the distribution of roots may be an additional strategy for managing the physiological salt balance of *A. marina* mangrove trees (Ridd, 1996; McKee, 2001).

There was significant variation in isotopic signa-tures of water sources between sites. The $\delta^{18}O$ of rainwater was lowest in the tidal creek and outer estuarine sites compared to the inner estuarine sites. Seawater and pore-water in Giralia Bay were more enriched in ^{18}O and exhibited higher salinity values than seawater and tidal water from the Moreton Bay and the Noosa River study areas (Fig. S1). These results reflect the high evaporative demand in the region (McGuire & McDonnell, 2007). Additionally, the highly saline and more ^{18}O enriched pore-water and seawater in Giralia Bay may also reflect the limited input of fresh water that limits ^{16}O sources (Wolanski, 1986).

Stem growth of mangroves was more rapid in the Noosa River, where conditions are less saline than in Moreton Bay. In both locations increasing rainfall led to increases in the size of the daily stem increments (Fig. 5). Fresh water is essential for maintenance of turgidity of cells and tissues, assuring the presence of a driving force for cell enlargement, stomata opening and therefore photosynthetic carbon gain (Pallardy, 2008). Additionally, rainfall is associated with higher humidity and lower leaf-air vapour pressure deficits (Lambers et al., 2008) that may also contribute to maintaining positive water balances in mangroves trees (Reef & Lovelock, 2014). Zero growth was also observed when rainfall was zero (Fig. 5). No growth and shrinkage of stems may indicate use of stored water in stems to support transpiration and carbon gain during periods without rain (Bucci et al., 2004; Vandegehuchte et al., 2014). Thick fibres and phloem tissue of *A. marina* may play a role in water storage in this species, which supports metabolic function (San-tini et al., 2012).

Conclusions

Our results show that the growth of *A. marina* trees is dependent on access to fresh water, whether rainwater, groundwater or surface water. Mangrove root distri-butions are likely to be responsive to the distribution of

fresh water in the environment and may be deployed preferentially in soil macropores in order to enhance access to ephemeral water sources as well as nutrients. Our results indicate that the proportion of fresh water that mangroves use is higher in mangroves with high fresh water availability compared to those that inhabit more saline, marine dominated settings. In addition, rainfall availability correlates with higher growth rates and therefore higher production in mangroves.

References

Alongi, D. M., 2009. The Energetics of Mangrove Forests. Springer, Dordrecht.

Alongi, D. M. & R. Brinkman, 2011. Hydrology and Biogeo-chemistry of Mangrove Forests. In Levia, F. D., D. Carlyle-Moses & T. Tanaka (eds), Forest Hydrology and Biogeo-chemistry. Springer, Dordrecht: 203–219.

Australian Bureau of Meteorology, 2014. Australian Bureau of Meteorology home page. Commonwealth of Australia: Canberra [Available at http://www.bom.gov.au]. Accessed 15 January 2014.

Ball, M. C., 1988. Ecophysiology of mangroves. Trees 2: 129–142.

Brunskill, G. J., A. R. Orpin, I. Zagorskis, K. J. Woolfe & J. Ellison, 2001. Geochemistry and particle size of surface sediments of Exmouth Gulf, Northwest shelf, Australia. Continental Shelf Research 21: 157–201.

Bucci, S. J., F. G. Scholz, G. Goldstein, F. C. Meinzer, J. A. Hinojosa, W. A. Hoffmann & A. C. Franco, 2004. Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. Tree Physiology 24: 1119–1127.

Clough, B. F., 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. Australian Journal of Plant Physiology 11: 419–430.

Dennison, W. C. & E. G. Abal, 1999. Moreton Bay Study. A Scientific Basis for the Healthy Waterways Campaign. Brisbane City Council, Brisbane.

Ellsworth, P. & D. Williams, 2007. Hydrogen isotope fractionation during water uptake by woody xerophytes. Plant and Soil 291: 93–107.

Eslami-Andargoli, L., P. Dale, N. Sipe & J. Chaseling, 2009. Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland Australia. Estuarine, Coastal and Shelf Science 85: 292–298.

Ewe, S., S. Sternberg & D. Childers, 2007. Seasonal plant water uptake patterns in the saline southeast Everglades ecotone. Oecologia 152: 607–616.

Hewson, I., J. M. O' Neil, J. A. Furhman & W. C. Dennison, 2001. Virus-like particle distribution and abundance in sediments and overlying waters along eutrophication gradients in two subtropical estuaries. Limnology and Oceanography 46: 1734–1746.

Humphreys, W. F., C. H. S. Watts, S. J. B. Cooper & R. Leijs, 2009. Groundwater estuaries of salt lakes: Buried pools of endemic biodiversity on the western plateau. Hydrobiologia 626: 79–95.

Hutchings, P. & P. Saenger, 1987. Ecology of Mangroves. University of Queensland Press, Brisbane.

Komiyama, A., K. Ogino, S. Aksornkoae & S. Sabhasri, 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. Journal of Tropical Ecology 3: 97–108.

Lagergren, F. & A. Lindroth, 2004. Variation in sapflow and stem growth in relation to tree size, competition and thinning in a mixed forest of pine and spruce in Sweden. Forest Ecology and Management 188: 51–63.

Lambs, L., E. Muller & F. Fromard, 2008. Mangrove trees growing in a very saline condition but not using seawater. Rapid Communications in Mass Spectrometry 22: 2835–2843.

Lambers, H., F. S. Chapin III & T. L. Pons, 2008. Plant Physiological Ecology. Springer, New York.

Larsen, G. R. & M. E. Cox, 2011. Hydrochemical and isotopic characterisation of groundwaters to define aquifer type and connectivity in a subtropical coastal setting, Fraser Coast, Queensland. Environmental Earth Sciences 64: 1885–1909.

Lin, G. & L. Sternberg, 1992. Effect of growth form, salinity, nutrient and sulfide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). Australian Journal of Plant Physiology 19: 509–517.

Lin G. & L. Sternberg, 1993. Hydrogen isotopic fractionation by plant roots during water uptake in coastal wetland plants In Ehleringer J. R., A. E. Hall & A. E. Farquhar (eds), Stable isotopes and plant carbon-water relations. Academic Press Inc, New York: 497–510.

Lovelock, C. E., M. C. Ball, I. C. Feller, B. M. J. Engelbrecht & M. L. Ewe, 2006. Variation in hydraulic conductivity of mangroves: Influence of species, salinity, and nitrogen and phosphorous availability. Physiologia Plantarum 127: 457–464.

McGuire, K. & J. McDonnell, 2007. Stable isotopes tracers in watershed hydrology. In Michener, R. & K. Lajtha (eds), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden: 334–373.

McKee, K. L., 2001. Root proliferation in decaying roots and old root channels: A nutrient conservation mechanism in oligotrophic mangrove forests? Journal of Ecology 89: 876–887.

McKee, K. L., I. A. Mendelssohn & M. W. Hester, 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. American Journal of Botany 75: 1352–1359.

Menezes, M., U. Berger & M. Worbes, 2003. Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North Brazil. Wetlands Ecology and Management 11: 233–242.

Morrisey, D., A. Swales, S. Dittmann, M. Morrison, C. E. Lovelock & C. Beard, 2010. The ecology and management of temperate mangroves. Oceanography and Marine Biology: An Annual Review 48: 43–160.

Pallardy, S., 2008. Physiology of woody plants. Academic Press, San Diego.

Parnell, A. C., R. Inger, S. Bearhop & A. L. Jackson, 2010. Source partitioning using stable isotopes: Coping with too much variation. PLoS ONE 5: e9672.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reef, R. & C. E. Lovelock, 2014. Regulation of water balance in mangroves. Annals of Botany. doi: 10.1093/aob/mcu174

Ridd, P. V., 1996. Flow through animal burrows in mangrove swamps. Estuarine, Coastal and Shelf Science 43: 617–625.

Santini, N. S., N. Schmitz & C. E. Lovelock, 2012. Variation in wood density and anatomy in a widespread mangrove species. Trees 26: 1555–1563.

Scholander, P. F., 1968. How mangroves desalinate seawater. Physiologia Plantarum 21: 251–261.

Semeniuk, V., 1983. Mangrove distribution in Northwestern Australia in relationship to regional and local freshwater seepage. Vegetatio 53: 11–31.

Smith, T. J. & N. C. Duke, 1987. Physical determinants of interestuary variation in mangrove species richness around the tropical coastline of Australia. Journal of Biogeography 14: 9–19.

Sternberg, L. & P. K. Swart, 1987. Utilization of freshwater and ocean water by coastal plants of Southern Florida. Ecology 68: 1898–1905.

Stieglitz, T. C., J. F. Clark & G. J. Hancock, 2013. The mangrove pump: The tidal flushing of animal burrows in a tropical mangrove forest determined from radionuclide budgets. Geochimica et Cosmochimica Acta 102: 12–22.

Susilo, A., P. V. Ridd & S. Thomas, 2005. Comparison between tidally driven groundwater flow and flushing of animal burrows in tropical mangrove swamps. Wetlands Ecology and Management 13: 377–388.

Upkong, L. E., 1991. The performance and distribution of species along soils salinity gradients of mangrove swamps in southeastern Nigeria. Vegetatio 95: 63–70.

Vandegehuchte, M. W., A. Guyot, M. Hubau, S. R. De Groote, N. J. De Baerdemaeker, M. Hayes, C. E. Lovelock & K. Steppe, 2014. Long-term versus daily stem diameter variation in co-occurring mangrove species: Environmental versus ecophysiological drivers. Agricultural and Forest Meteorology 192: 51–58.

Wei, L., D. A. Lockington, S. Poh, M. Gasparon & C. E. Lovelock, 2012. Water use patterns of estuarine vegetation in a tidal creek system. Oecologia 172: 485–494.

West, A. G., S. J. Patrickson & J. R. Ehleringer, 2006. Water extraction times for plant and soil materials used in stable isotope analysis. Rapid Communications in Mass Spectrometry 20: 1317–1321.

Wolanski, E., 1986. An evaporation-driven salinity maximum zone in Australian tropical estuaries. Estuarine, Coastal and Shelf Science 22: 415–424.

Ye, Y., N. F. Tam, C. Lu & Y. Wong, 2005. Effects of salinity on germination, seedling, growth and physiology of three salt-secreting mangrove species. Aquatic Botany 83: 193–205.