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Harvesting water from unsaturated atmospheres: deliquescence of salt secreted onto leaf surfaces drives reverse sap flow in a dominant arid climate mangrove, *Avicennia marina*

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Summary

- The mangrove *Avicennia marina* adjusts internal salt concentrations by foliar salt secretion. Deliquescence of accumulated salt causes leaf wetting that may provide a water source for salt-secreting plants in arid coastal wetlands where high nocturnal humidity can usually support deliquescence whereas rainfall events are rare. We tested the hypotheses that salt deliquescence on leaf surfaces can drive top-down rehydration, and that such absorption of moisture from unsaturated atmospheres makes a functional contribution to dry season shoot water balances.
- Sap flow and water relations were monitored to assess the uptake of atmospheric water by branches during shoot wetting events under natural and manipulated microclimatic conditions.
- Reverse sap flow rates increased with increasing relative humidity from 70% to 89%, consistent with function of salt deliquescence in harvesting moisture from unsaturated atmospheres. Top-down rehydration elevated branch water potentials above those possible from root water uptake, subsidising transpiration rates and reducing branch vulnerability to hydraulic failure in the subsequent photoperiod.
- Absorption of atmospheric moisture harvested through deliquescence of salt on leaf surfaces enhances water balances of *Avicennia marina* growing in hypersaline wetlands under arid climatic conditions. Top-down rehydration from these frequent, low intensity wetting events contributes to prevention of carbon starvation and hydraulic failure during drought.

Introduction

The soil–plant–atmosphere continuum or SPAC describes a pathway for water movement through plants in which liquid water is absorbed from soil by roots, transported to shoots, evaporates from wet surfaces within leaves and the water vapour then diffuses to the drier atmosphere. Water movement through the SPAC pathway is driven by a gradient from the least to the most negative water potential. However, more than 180 plant species in diverse biomes can also access atmospheric sources of water when environmental conditions reverse the water potential gradient, driving water movement through a continuum from the atmosphere to the plant, and ultimately into the soil (Dawson & Goldsmith, 2018; Berry *et al.* 2019; Schreel & Steppe, 2020). Such reversal of water movement can occur when water vapour concentrations in leaf intercellular gas spaces are less than those in the atmosphere (Vesala *et al.*, 2017; Cernusak *et al.*, 2018) or when plant surfaces become wet under saturated atmospheres by immersion in fog (Burgess & Dawson, 2004; Simonin *et al.*, 2009) or cloud (Oliveira *et al.*, 2014), interception of rainfall (Breshears *et al.*, 2008), or temperature-dependent condensation of dew (Munne-Bosch *et al.*, 1999). Much less attention has been given to understanding how leaf wetting events that are promoted under unsaturated atmospheres by the structure and chemical characteristics of leaf surfaces, such as capillary condensation among dense trichomes (Konrad *et al.*, 2015) or deliquescence of hygrophilic substances (Burkhardt, 2010), can also improve plant water balances in water-limiting environments.

Deliquescence is the dissolution of a hygrophilic particle in water vapour and occurs when the vapour pressure equals the equilibrium vapour pressure above a saturated solution of the dissolved substance (Zhao *et al.*, 2008). Deliquescence therefore depends strongly on humidity. At 20°C, for example, NaCl crystals begin to absorb water vapour when the relative humidity (RH) is *c.* 66% and the rate of water absorption increases with increasing humidity, dissolving the crystal and forming a saturated solution of the solute (i.e. 6.1 M NaCl) when RH is raised to the deliquescence point (DRH) of 75% (Langlet *et al.*, 2011). Deliquescence of salt mixtures, such as sea salt, is more complex and occurs between 80–85% RH at 25°C (Zeng *et al.*, 2013). Once deliquescence occurs, the solution will grow in volume, diluting solute concentrations provided the water potential of the solution is more negative than that of the atmosphere (Zhao *et al.*, 2008). Therefore, deliquescence can initiate harvesting of substantial amounts of water from unsaturated atmospheres. Indeed, salt-covered leaves of *Nolana mollis*, a salt-secreting shrub of the Atacama Desert, accumulated 3–13 μl water $cm^{-2}\ h^{-1}$ (equivalent to 0.46 to 2.01 mmol water $m^{-2}\ s^{-1}$) on leaf surfaces with increase in RH from 85 to 95%, respectively, while no water accumulated on leaves cleaned of surface salt (Mooney *et al.*, 1980). Therefore under highly humid conditions a salty leaf surface may induce a covering of liquid water under unsaturated atmospheres more frequently and for longer periods than leaves that depend on dew formation without surface salt facilitating deliquescence.

How might leaves access water that accumulates in saline solutions? Depending on physico-chemical characteristics of both the leaf surface and the solution, leaf surfaces can absorb surface water and dissolved solutes by diffusion across the cuticle (Kerstiens, 2006), stomata (Eichert *et al.*, 1998; Burkhardt *et al.*, 2012) and through epidermal structures such as trichomes (Raux *et al.*, 2020; Schreel *et al.*, 2020), scales (Wang *et al.*, 2016) and hydathodes (Martin & von Willert, 2000) that facilitate diffusion across leaf surfaces (Fernandez *et al.*, 2017). Deliquescence plays critical roles in beneficial uptake of fertilisers applied to leaves (Fernandez & Eichert, 2009; Burkhardt, 2010) and in deleterious uptake of aerosols such as pollutants (Burkhart & Eiden, 1994; Burkhardt *et al.*, 2018) and salt spray (Burkhardt *et al.*, 2012) that become deposited on leaves of sensitive species. For example, a sea salt solution, initiated by deliquescence of dried salt spray on a leaf surface, can diffuse across the cuticle and through stomatal pores into leaves of sensitive species, causing injury from accumulation of toxic salt concentrations and dehydration of the leaves (Burkhardt *et al.*, 2012). This scenario is likely to represent an extreme along a continuum in leaf capacity to resist uncontrolled, apoplastic uptake of saline solutions. At the opposite extreme, halophytic species subject to periodic immersion in highly saline water, and daily accumulation of high levels of salt on leaf surfaces through salt spray or salt secretion would be expected to minimise uncontrolled cuticular entry of salt or loss of water, two properties that are crucial to salt tolerance (Ball, 1988). Indeed, Fuenzalida *et al.* (2019) found that hydraulic conductance of shoot surface water uptake in *Avicennia marina* was inconsistent with dominance by cuticular permeability, instead appearing dominated by leaf surface permeability that varied with time and hydration, most likely due to differential contributions of epidermal features including trichomes (Nguyen *et al.*, 2017b) and salt secretion glands (Tan *et al.*, 2013) known to absorb water in *A. marina*.

Average foliar salt secretion rates of *A. marina* growing under highly saline and low humidity conditions (300 nmol NaCl $m^{-2}\ s^{-1}$) would alone deliver 1.5 g salt $m^{-2}\ d^{-1}$ to leaf surfaces (Ball, 1988) with additional salt deposited as salt spray. Epidermal salt secretion glands of *Avicennia marina* show oscillatory patterns of NaCl secretion (Chen *et al.*, 2010) similar to those of *A. officinalis* that intermittently reabsorb water released during salt secretion, with selective water uptake dependent on aquaporins and concurrent with upregulation of PIP2;1 expression (Tan *et al.*, 2013). These aquaporins have dual water and ion channels; water plus ions move through the large central pore of the tetramer while most water transport occurs through the four smaller, monomeric pores (Khourghi *et al.*, 2018). Separation of ion and water transport functions is achieved by individual regulation of the two pore types (Byrt *et al.*, 2017; Qui *et al.*, 2020). Oscillation between salt secretion and resorption of water released during secretion was interpreted as a means of conserving water, with salt secretion glands potentially recovering 1 l m^{-2} leaf area d^{-1} (Tan *et al.*, 2013). This capacity would also enable foliar uptake of atmospheric water that condenses on salty leaf surfaces. These observations invite the question: can salt deliquescence on leaf surfaces drive top-down rehydration in trees of *Avicennia marina*?

At least three species in the genus *Avicennia* can absorb liquid water from leaf or shoot surfaces (Tan *et al.*, 2013; Fuenzalida *et al.*, 2019; Hayes *et al.*, 2020). We focussed on *Avicennia marina*, one of the most salt tolerant and widely distributed of mangroves, and the dominant species in hypersaline coastal wetlands of tropical, arid Western Australia (Duke *et al.*, 1998) and other arid climate mangrove systems, for example the Red Sea (Almahasheer *et al.*, 2016). The ^{18}O isotopic composition of *A. marina* stem water indicates the use of fresh and marine water sources (Lovelock *et al.*, 2017) with use of freshwater increasing with its availability from rainfall (Santini *et al.*, 2015). The water relationships of *A. marina* leaves revealed that uptake of atmospheric water was needed to account for more than 50% of the water required to raise leaf water potentials from the turgor loss point to full hydration (Nguyen *et al.*, 2017b). Furthermore, this requirement for absorption of atmospheric water increased with increase in the salinity and aridity of the environment in which the plants grew naturally (Nguyen *et al.*, 2017a), implying a critical role in maintenance of plant function. Indeed, rehydration by uptake of liquid water from shoot surfaces reverses diurnal dehydration-induced losses in leaf hydraulic conductance in *A. marina* (Fuenzalida *et al.*, 2019). Over longer periods, absorption of intercepted rainfall by *A. marina* enhances shoot hydration above that possible for plants growing in highly saline soil, providing the turgor pressure needed for episodic growth in response to storm events (Steppe *et al.*, 2018; Schreel *et al.*, 2019). However, major gaps exist in our knowledge of the extent to which *A. marina* may also rely on accessing atmospheric water from unsaturated atmospheres and the roles that such water acquisition may play in maintenance of physiological function.

The present study addressed shoot water uptake by *Avicennia marina* through field-based studies of sap flow characteristics and shoot water relationships under dry season conditions in a natural stand of mangroves growing under hypersaline conditions along Giralia Bay in arid Western Australia. We tested the hypotheses: (1) that deliquescence of salt secreted onto leaf surfaces can drive top-down rehydration; and (2) that absorption of atmospheric water from wetting events makes a functional contribution to shoot water balances, subsidising transpiration and reducing stem vulnerability to hydraulic failure.

Materials and Methods

Site characteristics

The study was conducted at Deep Creek, which drains into Giralia Bay in the arid tropics of Western Australia (22°27′34.0″ S; 114°14′31.9″E). The site was dominated by *Avicennia marina* (Forssk.) Vierh subsp. *marina* (Duke, 1991; Li *et al.*, 2016). These single-bole trees (height *c.* 3 m) were growing on an eroding chenier ridge, in sandy soil mixed with fine sediments and shell debris, at an elevation subject to daily tidal inundation. Salinity of surface water and soil pore water at a 30 cm soil depth (McKee, 1993) beneath each tree was measured with a hand-held refractometer.

Study design

Three trees of similar height and canopy structure were studied. Four branches of similar size were selected on each tree and assigned randomly to four treatments from this point forwards known as Natural, Wet, Dry and Ambient (Table 1). All branches supported foliage in the uppermost canopy that was fully exposed to direct sunlight on the north facing side of the tree. A sap flow meter (SFM1, ICT International Pty Ltd, Armidale, NSW, Australia) was installed (sensor depth 12.2 mm) in the leafless region of each branch near its junction with the main stem, *c.* 70–80 cm from the branch canopy. Branch level sap flow was monitored using the heat ratio method (Burgess *et al.*, 2001) in association with micrometeorological measurements to enable analyses of directional water fluxes in relation to air humidity, air temperature and the occurrence of wetting events due to deliquescence, dew or precipitation. Environmental data were recorded at 10-min intervals throughout the study by a portable weather station (Kestrel 3500 Delta T Meter; Neilsen–Kellerman Co., Boothwyn, PA, USA). Air vapour pressure deficit (VPD) was calculated according to Murray (1967): $\mathrm{VPD} = \mathrm{Pv} - ((\mathrm{RH}/100) \times \mathrm{Pv})$, where air temperature (Ta) and RH were recorded and vapour pressure (Pv) was calculated as $\mathrm{Pv} = 0.611 \exp(17.27\ \mathrm{Ta}/(\mathrm{Ta} + 237.3))$.

Detection of top-down rehydration events was based on reversal of sap flow, indicating downward movement of water from branches to the main stem. Branches were harvested when the study concluded, and zero flow baselines were determined for each meter/branch combination using the method recommended by the manufacturer. All leaves were harvested from each branch and imaged for determination of leaf area using IMAGEJ software (Schneider *et al.*, 2012). Total leaf dry mass was measured with a field balance (XP 205 Metter Toledo balance, Mettler–Toledo Ltd, Greifensee, Switzerland) after oven drying at 80°C for 72 h. Fresh transverse sections were cut from each stem adjacent to the position of the sap flow probes, stained with 0.01% (w/v) toluidine blue in tap water and imaged (Nguyen *et al.*, 2017a).

Monitoring sap flow under natural conditions

Sap flow was monitored in relation to natural variation in weather conditions in all four branches in each of the three trees at 20-min intervals for 7 d with one partial interruption. During the manipulation experiment, monitoring continued only in branches allocated to the Natural treatment (one branch per tree) from 18:00 h on 16 July 2015 until 07:30 h on 17 July 2015, and then resumed in all branches. In contrast with branches in the manipulation experiment, those in the Natural treatment remained untouched throughout the whole monitoring period.

During one afternoon, a sudden change in the weather provided an opportunity to study leaf rehydration during a natural foliar wetting event driven by salt deliquescence on leaf surfaces. Once water began to accumulate on leaf surfaces, leaves were harvested for measurement of water content and water potential (Ψ_{Leaf}) from branches adjacent to those monitoring sap flow. One leaf was harvested from each of the three replicate trees at each time point. Leaf fresh mass was measured before wrapping the leaf in plastic film and determining Ψ_{Leaf} with a Scholander pressure chamber (1050D; PMS Instruments, Albany, NY, USA), followed by measurements of leaf area and dry mass. These data were used to estimate leaf relative water contents based on additional data collected concurrently for construction of leaf pressure/volume curves (Nguyen *et al.*, 2017b). Measurements continued until light became too low to work (18:20 h). However, one twig with two fully expanded leaves was collected from each of the three trees to measure water uptake by detached

Table 1 Branch traits of *Avicennia marina* trees growing naturally in a coastal forest along Giralia Bay in arid Western Australia (mean ± SE, $n = 3$ trees).

Treatment	Total leaf area (cm^2)	Total leaf dry mass (g)	Leaf mass per area ($\mathrm{g\ m}^{-2}$)	Stem wood density ($\mathrm{g\ cm}^{-3}$)	Stem transverse area (mm^2)
Natural	1914.9 ± 320.5	67.9 ± 9.6	356.4 ± 13.1	0.66 ± 0.01	359 ± 38
Ambient	1295.5 ± 177.8	45.1 ± 5.5	349.8 ± 12.3	0.65 ± 0.01	349 ± 58
Dry	1546.9 ± 243.6	55.0 ± 7.3	359.0 ± 22.8	0.65 ± 0.01	400 ± 12
Wet	1757.1 ± 387.1	62.4 ± 15.1	353.5 ± 15.3	0.65 ± 0.01	357 ± 31

leaves. The twig was trimmed to a maximal branch length of *c.* 3 mm. The cut twig surface was sealed with superglue and wrapped securely with parafilm while the attached leaves were loosely wrapped with paper towels moistened with tap water. Each twig was sealed in an individual zip-lock plastic bag for transport 30 km to the field station. At 19:30 h, after 60 min total incubation under darkness at ambient temperature, twigs were removed from the bags and blotted dry. One leaf was cut in air from each twig, and fresh leaf mass was measured before determining Ψ_{Leaf}. Images were taken for determination of leaf area and leaves were then dried to determine dry mass. These data were used to calculate rates of rehydration and water uptake by leaves on detached twigs by assuming that their starting points were the same as those measured at the time of twig collection (18:20 h).

Monitoring sap flow under manipulated conditions

Conditions were manipulated on 1 d to assess effects of nocturnal Dry, Wet and Ambient treatments on branch sap flow, water relations of leaves and twigs, and gas exchange characteristics under common ambient conditions during the following photoperiod. In the late afternoon, six twigs of similar orientation (length 8–10 cm, and bearing 4–6 fully expanded leaves) were selected on each of the three treatment branches on each tree and allocated to one of six sampling times for measurement of gas exchange and diurnal variation in Ψ_{Leaf}. The two youngest, fully expanded leaves on each twig were allocated to either transpiring or nontranspiring treatments. The latter treatment was tightly covered with plastic cling wrap and an outer layer of aluminium foil. Branch treatments were then imposed just before sunset. Wet branches were doused with freshwater to fully wet all leaf and branch surfaces. Six soaking wet sponges each containing *c.* 100 g of water were distributed near the designated twigs. Then each branch was sealed inside a heavy gauge black garbage bag. Dry branches each received six envelopes made of 30% shade cloth containing 150 g of dried silica gel. The envelopes were secured near the twigs, and the branches were then covered with a heavy gauge black garbage bag, which was then purged with several volumes of dry, compressed air from a scuba tank before the garbage bag was sealed. Ambient branches were left exposed to natural conditions. Each branch was fitted with an *i*-button (Hygrochron DS1923, Whitewater, WI, USA) placed in a sheltered canopy position to monitor humidity and temperature during nocturnal treatments. Branches were liberated from Wet and Dry treatments at sunrise (07:30 h) by removing the garbage bags, sponges and envelopes containing silica gel.

Water potentials of paired transpiring and nontranspiring leaves from the designated twigs were measured at six sampling times arrayed at 2-h intervals from 30 min after sunrise, 08:00 h, to 18:00 h to assess effects of nocturnal treatments on branch water status under common conditions in the subsequent photoperiod. At each sampling time, the designated leaves were collected by severing petioles from their twigs with a sharp razor blade, wrapping the severed leaf tightly in cling wrap, and sealing each wrapped leaf in individual zip-lock plastic bags that were then stored in darkness in an insulated container. Water potential measurements were made within minutes of collection at a field laboratory established *c.* 20 m from the study trees. Measurements of leaf fresh mass were followed sequentially by measurements of Ψ_{Leaf}, area and dry mass, as described above.

Gas exchange measurements were made on fully expanded leaves during 10:30 h to 15:00 h with an IRGA Li-6400XT (Li-Cor Inc.). The flux was set to 500 ml min^{-1} and leaves were illuminated with a saturating PPFD of 1000 $\mu\mathrm{mol\,m}^{-2}\,\mathrm{s}^{-1}$. Leaf temperature, leaf-to-air VPD and the $\mathrm{CO_2}$ concentration were consistent with ambient conditions, with the registered values ranging from 22–25°C, 0.67–1.4 kPa and 418–426 μmol $\mathrm{CO_2}$ mol^{-1} air, respectively. Measurements were made on four different leaves on each of the Wet, Dry and Ambient treatment branches on each of the three trees.

Statistical analyses

Data were analysed by linear regression and ANOVA using SIGMASTAT 4.0 software (Systat Software Inc., San Jose, CA, USA). Reported values correspond to the average of the measurements made on each of three different trees. Data were subjected to a one-way nested ANOVA in which the factor was the manipulative treatment nested in a tree. Model assumptions were checked for normality (Shapiro–Wilk test; $P < 0.05$) and homogeneity of variances (Brown–Forsythe test; $P < 0.05$). Unless stated otherwise, the *P*-value was 0.05 or less for all values reported as significant.

Results

Branch characteristics

There were no significant morphological differences between branches selected for Natural, Wet, Dry and Ambient treatments either within or between trees (Table 1). Most of the branch transverse area was occupied by vascular tissue, at least at the point of sap flow sensor insertion (Fig. 1) No evidence of xylem conduit occlusion was seen in any branch sections, suggesting that all of the tissue was functional.

Sap flow under natural conditions

Due to its coarse structure, the soil was well flushed such that there was no measurable difference between the salinity of surface and soil pore water, which remained at 46 ppt (equivalent to an osmotic potential of −3.2 MPa) throughout the study. For reference, standard seawater has a salinity of 35 ppt with an osmotic potential of −2.4 MPa.

Environmental conditions and sap flow velocities were recorded simultaneously under natural conditions for 7 d (Fig. 2). During this period, branches were subject to a natural sequence of dry and wet conditions. The sequence began with a dry diel period (17/18 July 2015) when positive sap flow velocities were recorded throughout the day and night. During the day, sap flow velocity averaged 5 cm h^{-1} with a peak of 7.5 cm h^{-1}

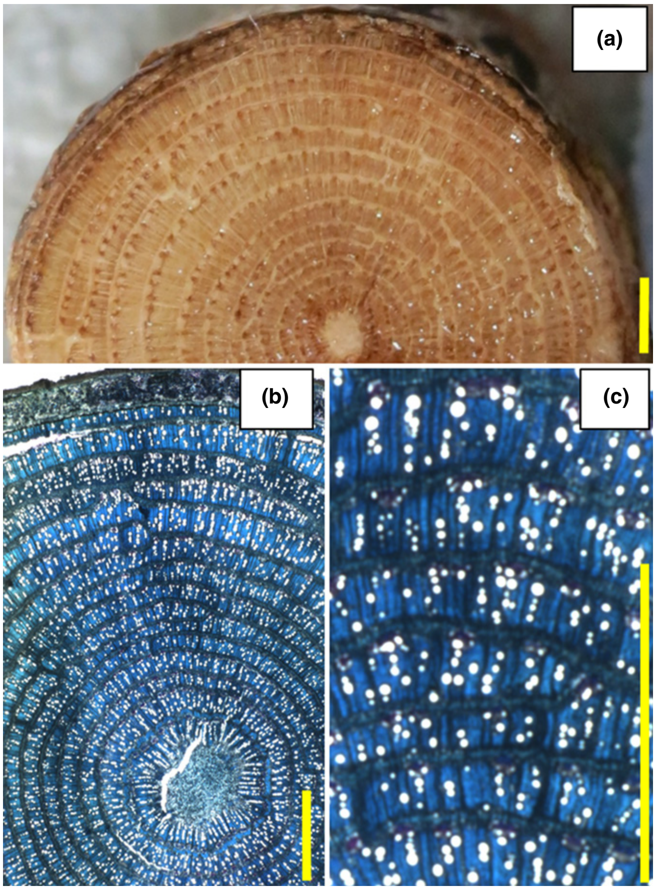


Fig. 1 Transverse sections adjacent to the position of sap flow measurement in a branch of *Avicennia marina* collected from Giralia Bay, Western Australia. (a) Fresh section and (b, c) fresh sections stained with 0.1% (w/v) toluidine blue in water. Note the unusual structure formed by successive cambia (Robert *et al*., 2011) with rows of xylem vessels (white circles) in bands of xylem (light blue) that alternate with bands of phloem (navy blue). The phloem bands branch intermittently, cross-linking successive bands to form a continuous tissue that connects across the width of the vascular area. Such cross-linkages between bands of phloem are visible in (a, b) and in the middle, lower right area of (c). Bars, 2.5 mm.

concomitant with a peak in air VPD driven by a rapid increase in air temperature from 18°C to 24°C. At night, RH averaged 75% (air VPD of 0.43 kPa) and sap flow velocity declined to 0.5 cm h^{-1}, 10% of the diurnal average.

The next night (18/19 July 2015), deliquescent conditions occurred when RH reached 85% and air VPD was 0.37 kPa (Fig. 2a,c). Reverse (i.e. negative) sap flow was recorded in three branches distributed in two trees, as shown in Fig. 3. Sap flow velocity averaged 0.6 cm h^{-1} from 19:00 h to 00:00 h (midnight), when a sudden increase in dew point (i.e. saturated vapour pressure) triggered a decline in sap flow velocity by 0.5 cm h^{-1} reaching zero velocity 1 h later (01:00 h). After 90 min at zero velocity, sap flow declined to a sustained negative velocity of −0.1 cm h^{-1} from 03:00 h to 07:00 h under deliquescent conditions (average RH of 82%; Fig. 2a) in the absence of dew, as shown by the 4°C difference between dew point and air temperatures during the time of reverse sap flow (Fig. 3a). This reverse flow velocity was 20% of the positive flow velocity that prevailed in the first 5 h of the dark period.

The next night, a greater average reverse flow velocity was recorded, reflecting the occurrence of reverse flow in all branches when RH reached 92% and air VPD was 0.30 kPa (Fig. 2). During this time, dew point temperature was 1.5°C lower than air temperature.

Deliquescence also drove reverse sap flow during the photoperiod, as shown during the late afternoon of 20 July 2015 (Fig. 2). Air temperature declined from 21.7°C at 16:00 h to 18.7°C at 18:20 h under overcast conditions, with a concomitant increase in RH from 66% to 82% and decrease in air VPD from 0.58 to 0.37 kPa (Fig. 4a). From 16:00 h to 17:40 h, sap flow velocity declined linearly at a rate of 2.2 cm h^{-1} from 3.8 to a plateau at 0.7 cm h^{-1} (Fig. 4b). This plateau began when water droplets first became visible on leaf surfaces at 17:36 h (Fig. 4b,d) and continued until 19:00 h (inset, Fig. 4b). While sap flow velocity at the branch base remained at 0.7 cm h^{-1}, Ψ_{Leaf} rose 1.5 MPa h^{-1} from −4.7 to −3.2 MPa and leaf relative water contents increased from 81.7 to 90.5% at 18:20 h (Fig. 4c). At 20:00 h, 2 h and 20 min after drops became visible on leaf surfaces, zero sap flow velocity was reached (inset, Fig. 4b). The velocity of reverse sap flow increased to a maximum of −0.4 cm h^{-1} 1 h later at 21:30 h (inset, Fig. 4b) and was sustained through the night (Fig. 4d). However, dew condensation is likely to have contributed to maintenance of reverse flow from 21:30 h onward (Fig. 2b) without change in sap flow velocity.

After sunset, further measurements of leaf water uptake were conducted on leaves of detached twigs. Water potentials of these leaves rose from −3.2 to −1.2 MPa after exposure of leaf surfaces for 1 h to liquid water through contact with wet paper towel (inset, Fig. 4c). These results showed that liquid water can be absorbed directly by leaf surfaces.

Finally, the greatest average reverse sap flow velocities of −0.8 cm h^{-1} occurred during intermittent precipitation on 20/21 July 2015 (Fig. 2) in which 5 mm of rainfall was recorded at Learmonth weather station, *c.* 38 km from the study site.

Pooling all data with the exception of those from the manipulative experiment, revealed a strong relationship between sap flow velocity and air VPD during both diurnal and nocturnal conditions (Fig. 5). Reverse sap flow was detected at a maximum air VPD of 0.3 kPa, a threshold corresponding to leaf wetting events (Fig. 2c). Reverse sap flow velocity became more negative with decreasing air VPD. Replotting all measurements of reverse sap flow as a function of RH showed that reverse sap flow velocities became increasingly negative as the intensity of wetting events progressively increased with RH through conditions conducive to deliquescence, dew and precipitation (Fig. 6). These results showed that absorption of moisture from unsaturated atmospheres can drive top-down rehydration in *Avicennia marina.*

Sap flow under experimental manipulation of nocturnal conditions

Relative humidities averaged (±SD) 39 ± 3.8, 75 ± 4.5 and 92 ± 2.9% during the Dry, Ambient and Wet nocturnal

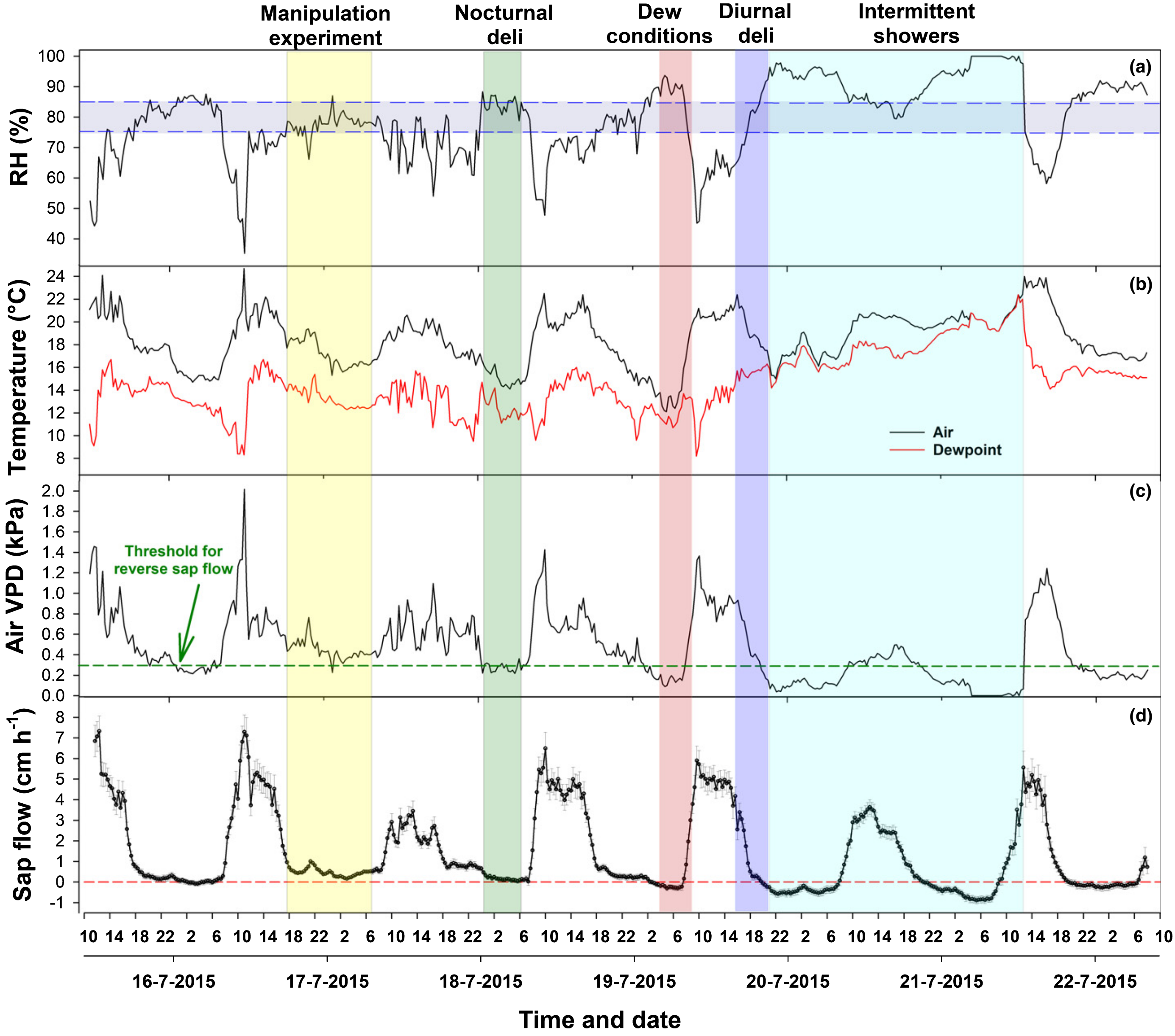


Fig. 2 Variation in natural environmental conditions and sap flow velocity in branches of three adjacent Avicennia *marina* trees over 7 d consecutively in a coastal forest along Giralia Bay, Western Australia. Vertical coloured bands indicate key periods during the study. The yellow band indicates the occurrence of an experiment when nocturnal conditions were manipulated (see Figs 7, 8). Sap flow data from branches used in the manipulation experiment were not included in the data shown for the yellow period. Other vertical bands indicate natural conditions that caused wetting events due to nocturnal deliquescence (green), dew (brown), and diurnal deliquescence (purple) preceding dew and intermittent showers (blue). See further details in Fig. 6. (a) Relative humidity of the air. Horizontal blue band indicates the range of conditions conducive to initiation of deliquescence of sea salt. (b) Air temperature (black line) and dew point (red line). (c) Vapour pressure deficit (VPD) of the air. Dashed green line indicates the threshold maximum at which reverse sap flow was detected (see Fig. 5). (d) Sap flow velocity as a function of time during the study period. Values are given as means ± SE, $n = 3$ trees. Four branches were measured per tree except during the yellow period when the measurements were made on the one branch per tree allocated to the Natural treatment.

treatments, respectively (Fig. 7a). While Wet leaves remained wet overnight, Ambient leaves experienced a gradual increase in RH that exceeded the threshold for sea salt deliquescence at *c.* 23:00 h (Figs 2a, 7a). These conditions persisted for the remainder of the night while air temperatures remained too high for dew formation (Fig. 2b). Air temperatures declined from 21 to 16°C with no significant differences between treatments (Fig. 7b). Therefore the enclosure of branches within the Dry and Wet treatments induced no measurable thermal insulation under the prevailing cloudy skies, and the responses to nocturnal conditions were independent of temperature differences between treatments.

Nocturnal sap flow velocity was affected by treatment conditions (Fig. 7c). Sap flow in Dry and Ambient treatments remained positive throughout the night and converged on an

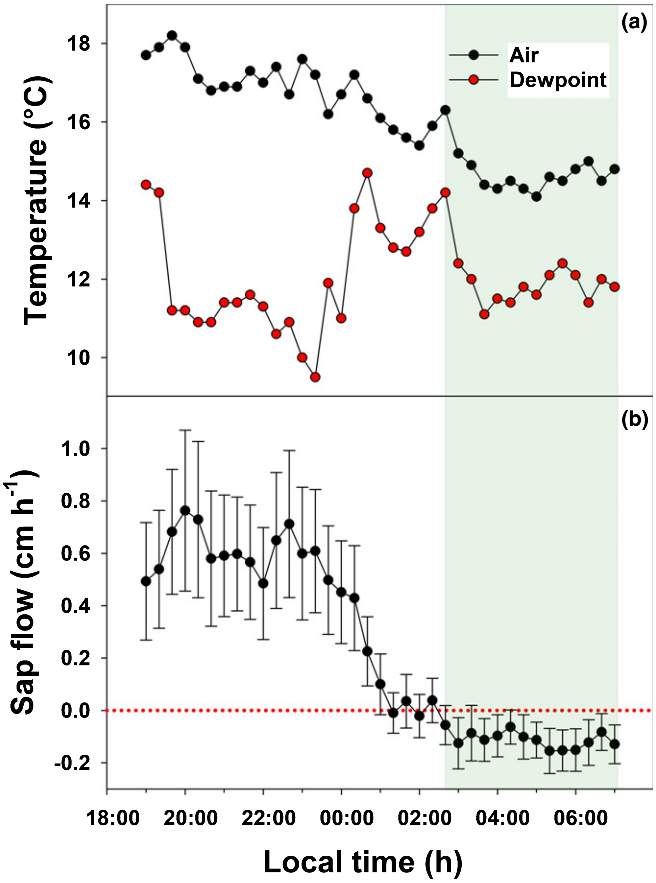


Fig. 3 Reverse sap flow in branches of *Avicennia marina* during a natural nocturnal deliquescence event in the absence of dew formation, corresponding to the period of the vertical green band shown in Fig. 2. Time-dependent variation in (a) air and dew point temperature, and (b) sap flow velocity in branches that exhibited reverse sap flow during the night. Values for sap flow velocity are given as means ± SE, $n = 3$. The vertical green band indicates conditions conducive to deliquescence of sea salt.

average velocity of 0.5 cm h^{-1}. In branches receiving the Wet treatment, sap flow velocity declined to zero cm h^{-1} 1 h after application of liquid water and 1 h later reached a maximum rate of negative flow (−0.5 cm h^{-1}), which was sustained for the rest of the night.

Leaf water potentials were highly variable upon liberation from nocturnal treatments at dawn. Consequently, there were no significant differences between those of covered and uncovered leaves, which averaged −1.5 ± 0.2 MPa across all treatments (Fig. 8), higher than expected from equilibrium with the soil water (salinity 46 ppt, osmotic potential −3.2 MPa).

Nocturnal treatments differentially affected leaf and branch water storage which was depleted during the subsequent photoperiod (Fig. 8a–c). Specifically, Ψ_{Leaf} of transpiring leaves in all treatments remained higher than that of soil water (Ψ_{Soil}) for an average of 2 h ± 26 min, and then declined gradually to minimum values near the average turgor loss point of −4.9 ± < 0.05 MPa determined by Nguyen *et al.* (2017a). By contrast, Ψ_{Leaf} of nontranspiring leaves, here interpreted as measures of branch water potentials (Ψ_{Branch}) adjacent to the transpiring leaves, remained elevated above Ψ_{Soil} for 4 h ± 35 min in Dry and Ambient treatment branches and declined to minimum values that were generally 0.5 MPa more negative than Ψ_{Soil}. In Wet branches, Ψ_{Branch} remained elevated above Ψ_{Soil} for 7 h ± 39 min and declined to a minimum *c.* 1 MPa more negative than Ψ_{Soil} at 18:00 h.

There were no significant differences in the daytime gas exchange characteristics of leaves from branches that had received different nocturnal treatments. Photosynthetic CO_2 assimilation rates and stomatal conductance averaged maximum values of 9.5 ± 0.15 μmol CO_2 m^{-2} s^{-1} and 0.3 ± 0.02 mol m^{-2} s^{-1}, respectively, in leaves of branches from all treatments. Similarly, there were no detectable differences between daytime sap flow velocities in branches following different nocturnal treatments (Fig. 8d).

Discussion

The present study expands our knowledge of water sources accessed by *Avicennia marina* to include water harvested from unsaturated atmospheres through deliquescence of salt that accumulates on leaf surfaces by secretion and deposit of salt spray. Leaf wetting events occurred when liquid water accumulated on shoot surfaces through interception of rainfall, condensation of dew and deliquescence of salt. Water uptake during these events could drive top-down rehydration as demonstrated by reversal of sap flow (Fig. 2). Precipitation produced the highest reverse sap flow rates (Fig. 6), possibly reflecting the areal extent and duration of wetting of absorptive surfaces with water of the highest osmotic potential. However, precipitation events occur at the lowest frequency in arid, coastal climates. The second highest rates of reverse sap flow occurred during conditions conducive to dew formation (Fig. 6), possibly reflecting the areal extent of canopy surface temperatures that reach dew point during nocturnal chilling. Finally, the lowest average rates of reverse sap flow occurred in response to deliquescence of salt on leaf surfaces (Fig. 6). Rates of liquid water accumulation following deliquescence of surface salt would be limited by water vapour diffusion to sites of deliquescence, while rates of leaf water uptake by aquaporin channels in salt secretion glands (Tan *et al.*, 2013) would depend on accumulation of sufficient water for osmotic potentials of the surface solution to become favourable for diffusion of liquid water into the leaf (Tyerman, 2013). Both rates of surface water accumulation (Zhao *et al.*, 2008) and rates of foliar water uptake would be enhanced by increase in RH above the deliquescence point. This may explain the increasingly negative reverse sap flow velocity as RH increased from 70 to 90% in *Avicennia marina* (Fig 6), and in another salt-secreting woody species of arid areas, *Tamarix ramosissima* (Li *et al.*, 2014). An RH of roughly 80% is often measured at a standard 2 m height above oceans and coastal waters (Pfahl & Niedermann, 2011; MacKellar *et al.*, 2013; Lainé *et al.*, 2014), implying that humidity within mangrove vegetation will often be conducive to deliquescence of NaCl (Langlet *et al.*, 2011) and sea salt (Zeng *et al.*, 2013). Therefore, despite driving the lowest intensity of wetting events,

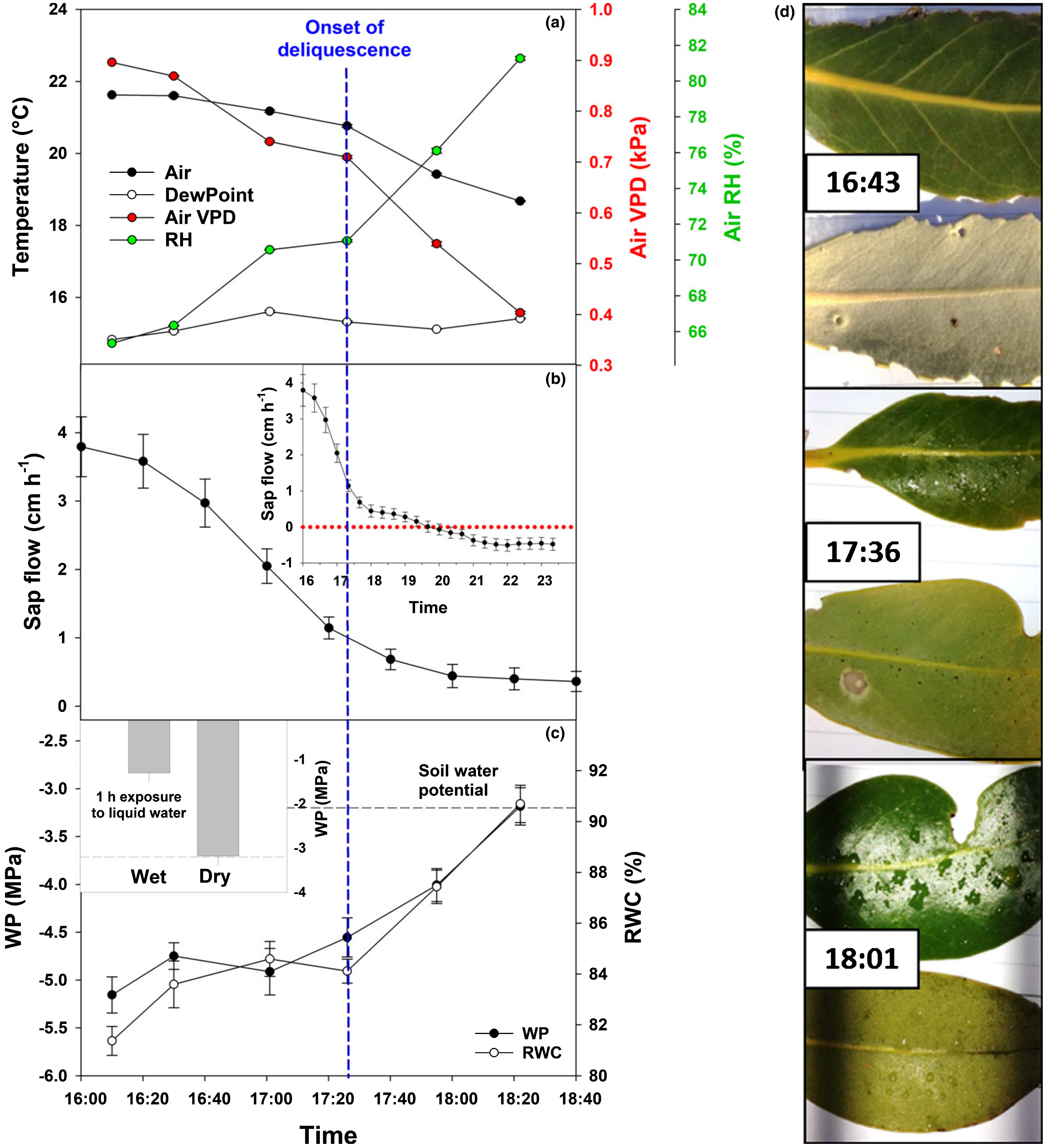


Fig. 4 Reversal of sap flow velocity in branches of *Avicennia marina* during a diurnal deliquescence event, corresponding to the period of the vertical purple band shown in Fig. 2. (a) Temperature and dew point of the air, together with the vapour pressure deficit (VPD) of the air and the relative humidity of the air from 16:00 h to 18:40 h. (b) Branch sap flow velocity from 16:00 h to 18:40 h in the large panel, with the inset showing an expanded plot from 16:00 h to 23:30 h. Values are given as means ± SE, $n = 3$ trees. (c) Water potential and relative water content (RWC) of leaves harvested at time points from 16:10 h to 18:25 h in the large panel. Inset shows leaf water potentials measured after detachment at 18:25 h (Dry) and after incubation of detached leaves in wet paper towels for 1 h (Wet). All values are given as means ± SE, $n = 3$ trees. Horizontal black dashed line shows the water potential (−3.2 MPa) of pore water from a soil depth of 30 cm. Vertical blue dashed line indicates the onset of deliquescence. (d) Images of upper and lower leaf surfaces before (16:43 h) and during (17:36 h and 18:01 h) the deliquescence event. Note the development of water drops on the upper (dark green) leaf surface and the change in colour from white to green as the trichomes covering the lower leaf surface become filled with water.

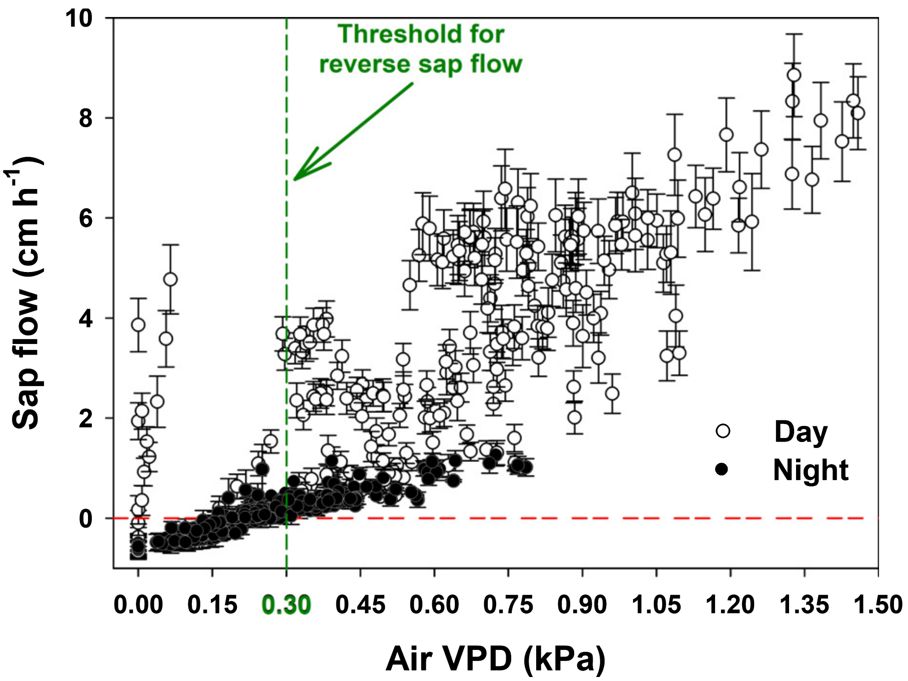


Fig. 5 Branch sap flow velocity of *Avicennia marina* during day (open circles) and night (filled circles) as a function of natural variation in vapour pressure deficit of the air (VPD). Values are given as means ± SE, $n = 3$ trees, and correspond to the data shown for 7 d consecutively in Fig. 2. The threshold indicates the maximum VPD at which reverse sap flow was detected. Lines drawn by linear regressions for day (sap flow velocity = −1.0277 + 6.0867 VPD; $r^2 = 0.71$, $P < 0.0001$) and night (sap flow velocity = −0.5125 + 2.3468 VPD; $r^2 = 0.84$, $P < 0.0001$).

the high frequency of deliquescent conditions and extended duration of conditions promoting growth of the initial deliquescent solution enable salt-secreting leaves to harvest substantial quantities of liquid water from unsaturated atmospheres. The congruency between theoretical underpinnings of salt deliquescence and the conditions promoting reverse sap flow under unsaturated atmospheres (Fig. 6) strongly support the hypothesis that condensation initiated by deliquescence of salt secreted onto leaf surfaces can drive top-down rehydration in *Avicennia marina*.

Observations of shoot rehydration in response to rapid change in microclimatic conditions, as occurred during the deliquescence event shown in Fig. 4, underscored the complexity of water relations in a species with simultaneous access to multiple water sources. Rehydration, here indicated by increase in Ψ_{Leaf}, began in the late afternoon when evaporative demand declined with increase in ambient vapour pressure (Fig. 4a). At this time, Ψ_{Leaf} averaged −4.7 MPa, near the turgor loss point of −4.9 MPa measured in adjacent trees of *A. marina* (Nguyen *et al.*, 2017a). With such low Ψ_{Leaf}, it is likely that some sap flow was not driven by transpiration, but contributed to shoot rehydration. Leaf water potential began to increase when atmospheric RH reached 72% (Fig. 4a), consistent with onset of NaCl deliquescence (Zeng *et al.*, 2013) and coincident with the appearance of wet leaf surfaces (Fig. 4d). Within 50 min, Ψ_{Leaf} rose by 1.5 MPa to −3.2 MPa, the level of Ψ_{Soil} (Fig. 4b,c). During this time, the sap flow rate from the main stem into the branch averaged 0.65 cm h^{-1} while deliquescent wetting was visible on the leaves, suggesting that branch rehydration may have occurred from two directions (Goldsmith, 2013).

Leaf rehydration to Ψ_{Leaf} higher than that of Ψ_{Soil} (−3.2 MPa) would have relied on the uptake of vapour and liquid water that accumulated following deliquescence of salt on leaf surfaces while air temperatures remained above dew point (Fig. 4a). Separate measurements showed that average rates of rehydration in detached leaves (2 MPa h^{-1}), when liquid water was sourced exclusively through the leaf epidermis (Fig. 4c, insert), were *c.* 30% greater than rates in attached leaves (1.5 MPa h^{-1}, estimated as Ψ_{Leaf} rose to the level of Ψ_{soil} while sap flow was positive) (Fig. 4c). Assuming an average leaf water storage capacitance of 1.00 ± 0.11 mol m^{-2} MPa^{-1} measured in adjacent trees for the range of Ψ_{Leaf} over which change in Ψ_{Leaf} was dominated by variable turgor (Nguyen *et al.*, 2017a), the equivalent rate of leaf surface water uptake calculated for detached leaves was *c.* 0.56 mmol m^{-2} s^{-1}. This estimate is within the range of values reported for leaves of a different subspecies from the wet tropics, *A. marina* ssp. *eucalyptifolia* (Fuenzalida *et al.*, 2019), and accords well with the average rate of water uptake by salt secretion glands per leaf area (0.64 mmol m^{-2} s^{-1}) in *Avicennia officinalis* (Tan *et al.*, 2013). Several processes may have contributed to more rapid rates of rehydration in detached than attached leaves in the present study. For example, water may have accumulated more rapidly within detached leaves because water transport to more dehydrated stems was blocked. It is also possible that hydraulic conductance to foliar water uptake increased with leaf hydration. This could occur, for example, through increase in the number and activity of aquaporins that modulate water movements across cell membranes (Chaumont & Tyerman, 2014), while

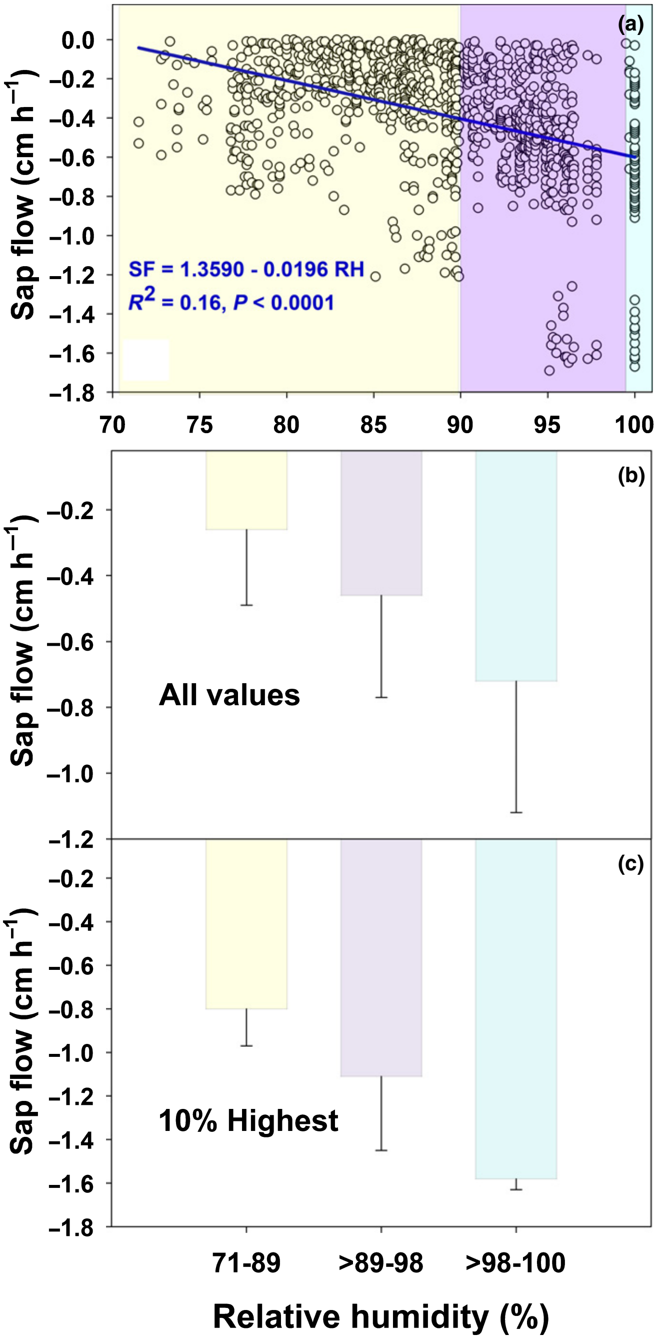


Fig. 6 Reverse sap flow velocity in branches of *Avicennia marina* trees growing naturally in a coastal forest along Giralia Bay in arid Western Australia as a function of relative humidity. (a) Linear regression of all measurements of reverse sap velocity as a function of relative humidity at the time of measurement. Data were collected from four branches on each of three trees over the 7 d of sap flow monitoring shown in Fig. 2. Colour bands classify the data into three groups indicating conditions when leaves may have absorbed water that accumulated on leaf surfaces following deliquescence of salt (yellow, 71 to 89% RH), condensation of dew (purple, >89 to 98% RH), and interception of rainfall (blue, >98 to 100% RH). The threshold RH for dew formation was set according to predictions for clear night skies (Monteith, 1957), and may overestimate the occurrence of dew under the overcast conditions of the study. (b) Average reverse sap flow velocity ± SD for all data and (c) for the 10% highest data values in each of the three classifications shown in (a).

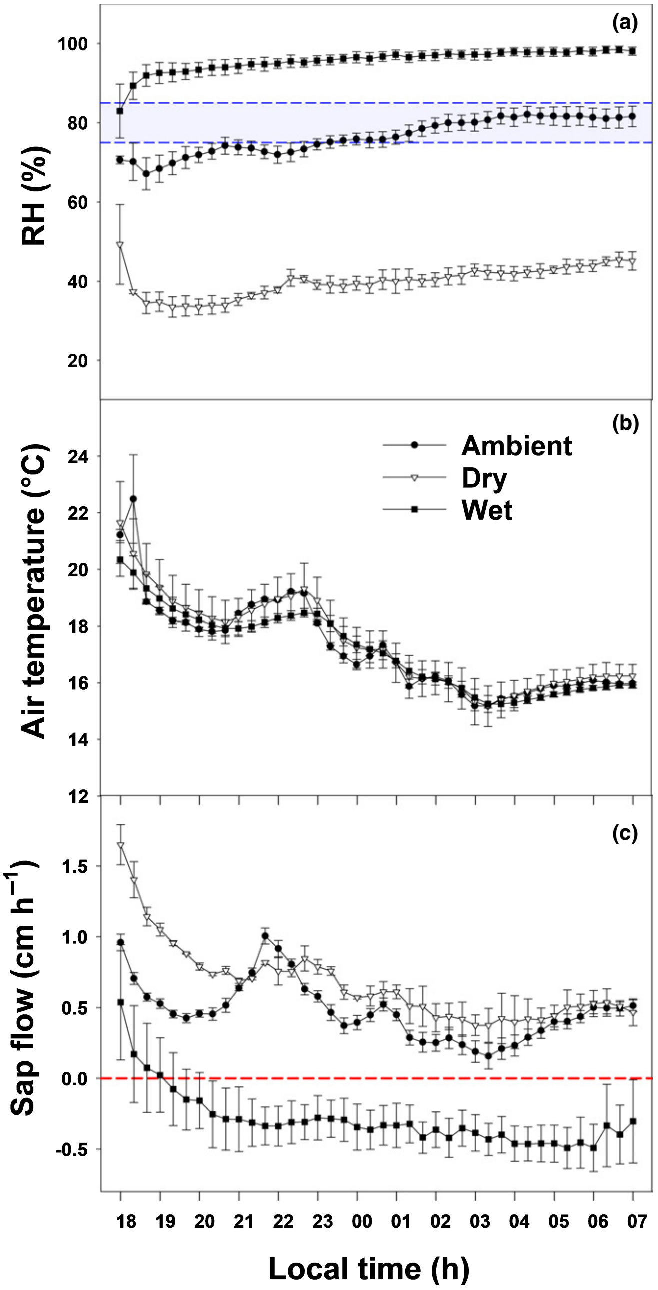
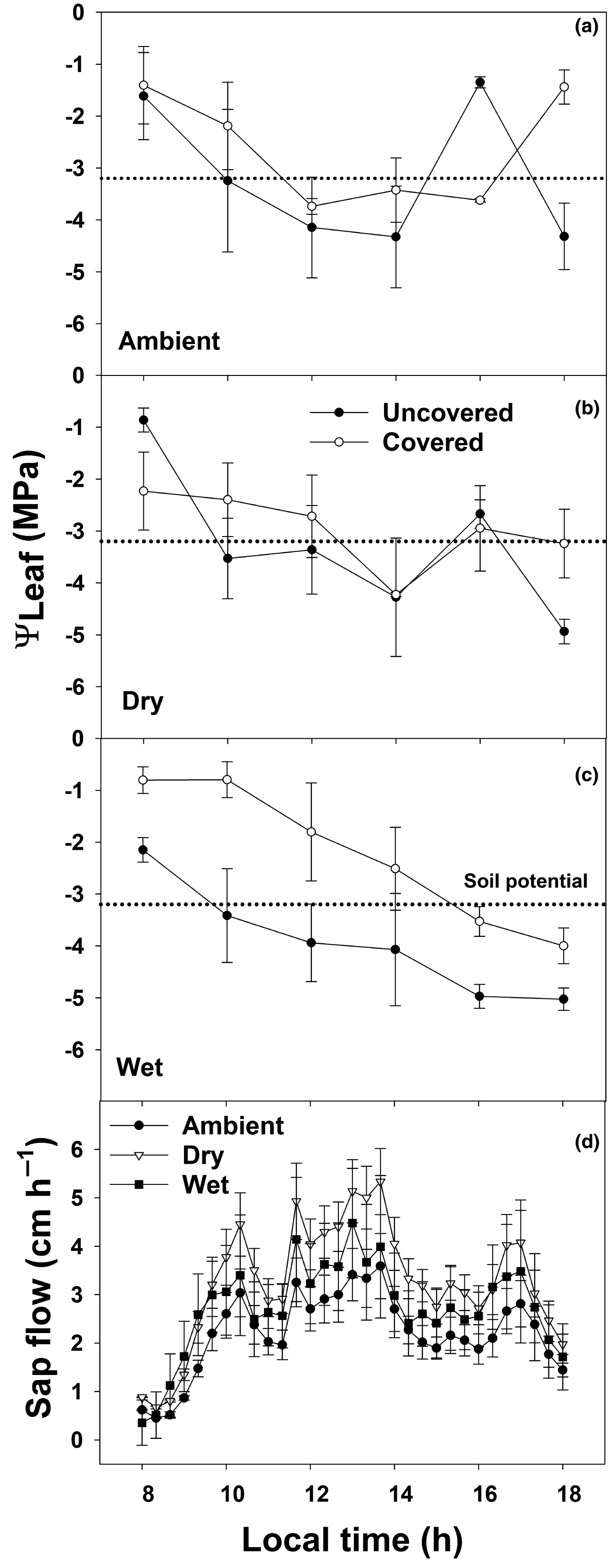


Fig. 7 Experimental manipulation of nocturnal sap flow in branches of *Avicennia marina* trees growing naturally in a coastal forest along Giralia Bay in arid Western Australia. (a) Relative humidity (RH), (b) air temperature, and (c) sap flow velocity as functions of time in bagged branches receiving Wet and Dry treatments and at positions adjacent to unbagged branches exposed to Ambient conditions. The blue bar indicates conditions conducive to deliquescence of sea salt. Values are given as means ± SE, $n = 3$ trees, each with three separate branches allocated to Wet, Dry or Ambient conditions.

reduction in cellular viscosity could enhance rates of water diffusion through the symplast (Sevanto, 2018). The whole sequence of events during shoot rehydration from Ψ_{Leaf} more negative than Ψ_{Soil} to higher values approaching saturation of leaf cellular water storage (Nguyen *et al.*, 2017a, b), highlights the complexity of processes driving fluxes from multiple water sources.



Hydraulic integration within the trees, each with a single main stem, was suggested by diurnal patterns in Ψ_{Leaf} following experimental imposition of nocturnal Wet, Dry and Ambient conditions on different branches of the same trees. The three treatments (Fig. 7a) were expected to produce differences in leaf hydration at dawn. However, shortly after sunrise, Ψ_{Leaf} of transpiring and nontranspiring leaves were elevated above Ψ_{Soil} (-3.2 MPa), averaging -1.5 ± 0.24 MPa across treatments (Fig 8). Nocturnal RH surrounding dry branches was too low for deliquescence of sea salts (Fig. 7a), the implication being that high Ψ_{Leaf} in dry branches may have resulted from importation of water from better hydrated regions of their trees. Indeed, sap flow data showed that Dry and Ambient branches imported water from main stems while Wet branches exported water to main stems throughout the night (Fig. 7c).

Leaf water potentials declined to the level of Ψ_{Soil} during the first 2 h of photosynthetic activity (Fig. 8). These results supported previous estimates that water absorbed from atmospheric sources and stored in leaves of *A. marina* could subsidise transpiration rates of 1 mmol m^{-2} s^{-1} without reliance on water sourced from roots for *c.* 2 h (Nguyen *et al.*, 2017a, b). Similarly, Lechthaler *et al.* (2016) found that most of the water used in gas exchange by seedlings of another mangrove, *Rhizophora mangle*, was discharged from storage within leaves and stems, particularly when soil water salinities were high. As carbon cannot be gained without water loss, the subsidy provided to transpiration by release of stored water absorbed from atmospheric sources could contribute a substantial carbon benefit to plants growing in hypersaline soil under arid conditions, enabling higher rates of carbon gain in the morning when air temperatures, and therefore also evaporative demand, would be lowest.

In contrast with the Ψ_{Leaf} of transpiring leaves, those of nontranspiring leaves remained elevated above Ψ_{Soil} for 6–7 h in Wet treated branches and 3–4 h in branches from Ambient and Dry treatments (Fig. 7a–c). These results showed that redistribution of water absorbed during partial wetting of a canopy, as might occur naturally during low intensity wetting events, enhanced rehydration and water storage in all canopy branches, but especially those under the wettest conditions. With the onset of rapid transpiration from leaves, discharge of stored water from living branch tissues would contribute to the transpiration stream while buffering against the development of tensions adverse to the maintenance of branch hydraulic function (Zweifel *et al.*, 2001;

Fig. 8 Effects of the nocturnal conditions shown in Fig. 7 on water relations and branch sap flow velocity in trees of *Avicennia marina* under common conditions in the subsequent photoperiod. Diurnal variation in the average water potential of paired transpiring (open circles) and covered, nontranspiring leaves (solid circles) of branches that had been exposed to (a) Ambient, (b) Dry or (c) Wet nocturnal conditions. Dotted horizontal line indicates the water potential (−3.2 MPa) equivalent to the salinity (46 ppt) of pore water extracted from a soil depth of 30 cm. (d) Diurnal variation in sap flow velocity of branches that had received Ambient, Dry or Wet nocturnal treatments. Values are given as means ± SE, *n* = 3 trees, each with three separate branches allocated to Wet, Dry or Ambient conditions.

Meinzer *et al.*, 2009; Sevanto *et al.*, 2011; Pfautsch *et al.*, 2015a, b). Branch hydraulic vulnerability was not measured in the present study. However, using the standard bench drying technique, 50% loss in hydraulic conductivity (PLC_{50}) occurred at −6 MPa in branches of *Avicennia marina* ssp. *australasica* growing in soil with a pore water salinity of 46 ppt (Martin, 2007), 3 ppt less than that of the present study (49 ppt). The average turgor loss point in leaves of these trees (−4.6 MPa) was not significantly different from the value of −4.9 MPa measured in leaves from trees at our study site (Nguyen *et al.*, 2017a). Assuming similar hydraulic vulnerability between the two subspecies growing in soils of similar salinity, leaf turgor loss occurs at a Ψ_{Leaf} *c.* 1.7 MPa more negative than Ψ_{Soil}, and branch PLC_{50} is likely to occur with further lowering of Ψ_{Branch} by 1.1 MPa to −6.0 MPa, *c.* 2.8 MPa more negative than Ψ_{Soil} (−3.2 MPa). The present study showed that absorption of atmospheric water enables sustained elevation of Ψ_{Branch} above that of Ψ_{Soil}, thereby increasing hydraulic safety margins and reducing the risk of hydraulic failure during rapid transpiration.

The results underscored a need to better understand the discharge and recharge of stem water storage. Sap flow rates, measured *c.* 80 cm from the canopy leaves, increased in all branches after 08:00 h, while Ψ_{Leaf} of transpiring and nontranspiring leaves were higher than Ψ_{Soil} (Fig. 8). Concurrent measurements of main stem diameter variation on adjacent trees revealed stem swelling from dawn through midday, with both the magnitude and daily pattern of stem swelling and shrinking persistent after total canopy defoliation (Vilas *et al.*, 2019). Their results are consistent with a point dendrometer study that identified bark tissue as the source of stem swelling in *A. marina* var. *australasica* (Barraclough *et al.*, 2019), presumably in response to osmotic adjustments of storage tissues (Vandegehutche *et al.*, 2014). Given the importance of stem capacitance in shoot function (Meinzer *et al.*, 2009), daytime swelling in *Avicennia marina* and other mangrove species (Vilas *et al.*, 2019) may relate to light-dependent maintenance of stem hydraulic function (Schmitz *et al.*, 2012), and merits further research.

Elevation of branch hydration above the level that could be provided by soil water, would also increase the magnitude and duration of turgor pressure (Nguyen *et al.*, 2017a, b). The longevity of elevated Ψ_{Branch} during dry season conditions of the present study was ephemeral, requiring daily shoot wetting events to raise Ψ_{Branch} and Ψ_{Leaf} above those that could be achieved by uptake of soil water alone (Fig. 8). Nevertheless, the frequent occurrence of low level wetting events of long nocturnal duration, as can occur following deliquescence of salt secreted onto leaf surfaces, may be important for the maintenance of cell and tissue functions, particularly the generation of turgor pressure required for growth (Steppe *et al.*, 2018; Schreel *et al.*, 2019) and phloem transport. Indeed, recent studies have pointed to the importance of the phloem in maintenance of hydraulic functions of the xylem during drought (Mencuccini *et al.*, 2015; Sevanto, 2018; Martinez-Vilalta *et al.*, 2019), and more research is needed to understand the role of top-down rehydration in the integration of vascular function.

Conclusion

Our study shows that condensation following deliquescence of salt secreted onto leaf surfaces of *Avicennia marina* can provide a source of water that can drive top-down rehydration under unsaturated atmospheres. As coastal humidity is frequently within the range supporting salt deliquescence, these wetting events may provide a water source that is critical for growth and survival of *Avicennia marina* where hypersaline conditions limit the capacity for water uptake by roots and arid climatic conditions limit opportunities for absorption of dew or water intercepted by shoots during rare rainfall events. Salt deliquescence creates frequent, low intensity wetting events of prolonged nocturnal duration that enable recharge of leaf and stem water storage to levels exceeding those possible through uptake of water from hypersaline soil water sources by roots. The storage is ephemeral, being discharged during the subsequent photoperiod, but nevertheless provides a substantial water subsidy that supports transpiration (and therefore also carbon gain) while buffering against excursions in stem water potentials to dangerously low levels. Foliar absorption of water that accumulates following salt deliquescence therefore contributes to water balances and dampens potential exposure to carbon starvation and hydraulic failure during drought.

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Author contributions

REC, MCB and HTN planned and designed the research. REC, MCB and HTN performed experiments, conducted fieldwork. REC and HTN analysed data. REC, MCB, HN, MM, RSO, LS and CEL contributed to writing the manuscript.

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Data availability

Data relating this article can be found at The Australian National University Data Commons Library (ANU Data Commons Identifier: anudc:6102; doi: 10.25911/6094cba509e75).

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