



Article Assessing the Relative Importance of Climatic and Hydrological Factors in Controlling Sap Flow Rates for a Riparian Mixed Stand

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Abstract: Evapotranspiration by phreatophytes in riparian zones makes up a large component of the water balance. However, our understanding of the relative importance of controlling factors such as climatic conditions, species type, depth to groundwater and distance to surface water in riparian zones remains a significant knowledge gap. A field experiment was conducted in an irrigated catchment in North Queensland, Australia, to investigate the factors controlling evapotranspiration by groundwater dependent trees. The sap flow of four tree species was measured, along with soil moisture, groundwater levels and local climatic conditions. The relative influence of species, hydrologic and climate factors, and measured variables were investigated with two non-parametric methods: random forest and Principal Component Analysis (PCA). Field monitoring data revealed differences in sap flow rates and diurnal sap flow trends between species. Distance from surface water explained the most variance in sap flow rates for some of the *Eucalyptus tessellaris* trees at this site reduced as groundwater levels declined. Overall, results demonstrate the value that can be gained from applying non-parametric methods, such as random forest and PCA, to investigate the relative importance of the factors influencing evapotranspiration.



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). **Keywords:** groundwater dependent ecosystem; phreatophyte; evapotranspiration; sap flow; random forest modeling

1. Introduction

Transpiration by groundwater dependent trees can make up a significant proportion of the water balance, particularly in riparian areas [1,2]. However, transpiration by phreatophytes is often not measured as part of groundwater balance studies. Therefore, quantifying the water used by different tree species is an important component of groundwater dependent ecosystem studies [3].

A range of approaches are used to approximate the relationships between depth to groundwater and evapotranspiration (ET) by phreatophytes. These approaches vary from assigning "typical" ET rates based solely on the observed depth to groundwater, where an evapotranspiration range of 100–1000 mm/year is applied when the water table is 0–2 m below the ground surface [4] to developing ET curves, commonly either linear or segmented functions, which represent the relationship between depth to groundwater and ET rates [1].

As groundwater uptake by deep-rooted vegetation can be observed as a diurnal fluctuation in depth to groundwater, this fluctuation can be used to estimate groundwater uptake [5,6], providing that the specific yield of the aquifers can be estimated. In vegetated riparian zones, diurnal fluctuations in groundwater tables frequently occur [7]. However, the use of diurnal fluctuations for estimating groundwater uptake assumes that groundwater uptake diminishes or ceases at night [5]. Whilst nocturnal sap flow was largely regarded as insignificant prior to 2007, nocturnal sap flow has now been recognized as significant for some species [8,9]. In a review of 98 species and 246 datasets, nocturnal was found to constitute a particularly large proportion of total sap flow in tropical and equatorial regions, 16.54% and 29.10% of total sap flow, respectively [9]. Therefore, before applying water fluctuation-based methods, it is critical to investigate this assumption of zero nighttime water use [10].

More accurate quantifications of water use may be achieved by measuring transpiration for individual trees [3]. Tree water use can be quantified using multiple techniques that trace the movement of heat within the xylem [11,12]. One of these methods is the heat pulse method for measuring sap flow [11–13]. The heat pulse method is widely used in studies of groundwater transpiration by deep-rooted trees [3,13,14], yet, limited studies have quantified the differences in water use between species in mixed stands [15].

Groundwater transpiration has previously been found to be a function of depth to groundwater, maximum rooting depth for individual species, rooting distribution, and soil water reserves [14]. Doble and Crosbie [16] identified a wider range of potentially important factors in controlling groundwater transpiration, including climatic conditions, vegetation type, life stage of vegetation, maximum rooting depth, canopy cover, and soil type. Key climatic factors that control transpiration include Vapor Pressure Deficit (VPD), solar radiation, and air temperature [17,18].

Eamus, Zolfaghar, Villalobos-Vega, Cleverly, and Huete [13] also identified the important roles of aquifer attributes and environmental stress in controlling water use by groundwater dependent trees. In riparian zones, the distance from a river boundary has also been shown to be an important factor in controlling groundwater transpiration [19]. In that study, groundwater drawdown due to ET decreased with decreasing distance from the river boundary.

Whilst many factors have previously been identified as potentially important in controlling transpiration, what remains equivocal is which of these factors is the most important in a particular setting, and the relative importance of these factors.

To investigate the factors controlling transpiration by groundwater dependent vegetation, ecohydrological monitoring was carried out at a riparian field site in subtropical Australia. At this site, transpiration rates were determined for the following commonly occurring tree species in the region: *Eucalyptus tessellaris, Melaleuca dealbata, Pandanus cookie,* and *Acacia salicina*. Previous research has measured closely related species for some of these trees, such as *Eucalyptus grandis* [20], *Eucalyptus populnea* [21], *Melaleuca quinquenervia* [22], and *Melaleuca argentea* [23]. However, with the exception of the work by Madurapperuma et al. [24], little research has thermometrically measured sap flow rates in monocot species like *Pandanus cookii*. Therefore, this is the first study to publish transpiration measurements of the four species monitored in this study.

The selected field site is of particular interest because of ongoing efforts to improve the management of groundwater quantity and quality in the catchment. Transpiration at this riparian site is expected to be influenced by seasonally fluctuating groundwater levels in addition to groundwater–surface water interactions.

In this paper, we present a method for identifying the most important factors influencing transpiration in this mixed stand and quantifying the relative contributions of these factors. The specific research questions addressed through the combination of ecohydrological monitoring, principal component analysis, and random forest modeling were: (1) how does sap flow vary among species? (2) how does depth to groundwater affect sap flow rates? and (3) which factors are most important in influencing sap flow?

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2. Site Description

The Lower Burdekin covers approximately 2500 km² and is located on the northeastern coast of Queensland, Australia, directly adjacent to the Great Barrier Reef lagoon. Land use in the Lower Burdekin is dominated by irrigated sugarcane.

2.1. Climate

Average annual rainfall ranges from 890 to 1151 mm/year (for the period from 1890 to 2006, based on patched point datasets from the Bureau of Meteorology). The majority of the rainfall occurs during the summer months (December to February), and 75% of the annual rainfall occurs between December and March.

Annual pan evaporation, obtained from one climate station at Kalamia Estate in the Lower Burdekin, ranges from 1829 to 2315 mm, with a mean of 2057 mm (for the period 1 January 1958 to 29 February 2000). Measured temperatures for Kalamia Estate for the same time period range from an average daily minimum of 19 °C to an average daily maximum of 29 °C.

2.2. Hydrology and Hydrogeology

Three main surface water systems, the Burdekin River, Haughton River, and Barratta Creek system, drain the area and minor distributaries and other watercourses are located throughout the coastal plain. The floodplains associated with these systems have formed a flat to slightly undulating topography comprising alluvial and deltaic sediments. The Lower Burdekin floodplains comprise Quaternary sequences of gravel, sand, silt, clay, and mud, which were deposited throughout the formation of the delta by the actions of fluvial, tidal, and wave processes.

The field site is located close to Mt Inkerman. The site consists of a 125 m long strip of riparian vegetation adjacent to an artificial permanent wetland created through the construction of an earth dam further downstream. Similar to a significant proportion of riparian vegetation within the area, the site is found on the perimeter of sugarcane cultivated land in the Burdekin Delta. The groundwater levels in the region are less than 5 m from the surface, indicating that vegetation at the site is likely to be accessing groundwater. Moreover, the shallow water table and presence of a permanent wetland indicate a strong groundwater–surface water interaction.

The wetland at the site was a saltmarsh/floodplain area before agricultural development. The field site is found within a wetland complex that was previously listed on Australia's National Directory of Important Wetlands [25]. This wetland is disconnected from the tidal estuaries approximately 3 km away. The wetland was permanently saturated during the monitoring period as a result of agricultural drainage waters. However, several years after this study concluded, this site was returned to natural hydrological conditions by pumping accumulated water out of the wetland and then allowing the wetland to dry out in the dry season.

2.3. Soils

Soils in the Burdekin Delta were surveyed at a 1:50,000 scale in 2000. The soils at the ecohydrological monitoring site were mapped as a structured clay soil with no abrupt change in texture between A and B horizons. However, bore drilling logs from this site also indicate the presence of sandy layers within the top 2 meters of the sediment profile.

2.4. Vegetation

The predominant native vegetation types include eucalypt-dominated woodlands, native grasslands, riparian corridors, and wetlands. The field site was chosen as it represents the riparian vegetation found within riparian corridors across the Lower Burdekin, particularly within the estuarine wetland environment. The foliage projective cover of the vegetation is in the same range as most riparian vegetation within the region (20–55%).

The overstory at the site is dominated by the following native species; Moreton Bay Ash (*Eucalyptus tessellaris* F. Muell), Paperbark (*Melaleuca dealbata* S.T. Blake), Willow Wattle (*Acacia salicina* Lindl.), and Screw Pine (*Pandanus cookii* Martelli). Infrequent numbers of *Livistona australis* Mart., Pleigynium timorense Kunth and *Planchonia careya* (F. Muell.) R. Kunth are also scattered throughout the overstorey. The understorey is dominated by perennial native grasses and introduced weed and pest species, including *Cryptostegia grandiflora* R. Br. and *Chromolaena odorata* (L.) R.M. Kind & H. Rob.

The size and age class of each species at the site is varied, which allowed for classrelated effects and trends to be investigated. As the riparian strip chosen was relatively wide, this allowed for dominant species to be selected and monitored at a range of distances from the wetland. The ecosystem was in a healthy condition.

3. Materials and Methods

The majority of hydrological monitoring at the field site occurred from September 2011 to January 2012. This included monitoring of local climate, soil moisture, groundwater levels and both sap flow and tree growth for the dominant tree species at the site (Figure 1).



Figure 1. Site map showing locations of trees monitored, bores (labeled Bore1, Bore2, Bore3, Bore4, Bore5, Bore6), soil monitoring sites (labeled soil1, soil2, soil3, soil4, soil5) and the weather station, relative to the furrow irrigated sugarcane field on the west and the lagoon on the east. The individual tree IDs used for these species relate directly to the species name: *Eucalyptus tessellaris* (E1, E3, E4, E5 and E6), *Melaleuca dealbata* (M1, M2A, M2B and M3), *Pandanus cookii* (P1, P4 and P5), and *Acacia salicina* (A1, A2, A3, A4, A5 and A6).

3.1. Climate

An ICT International EnviroStation multi-parameter weather station was used to measure or calculate rainfall, vapor pressure deficit (VPD), solar radiation, wind speed, and wind direction with 16-bit resolution and between 1 and 3 percent accuracy. This weather station was located in an open area, close to the edge of the monitored trees (Figure 1). The climate monitoring occurred at 30 min intervals.

3.2. Tree Selection

Trees that were representative of native riparian vegetation across the Lower Burdekin were chosen such that results could be adapted for use across the region. The four dominant overstorey species were selected for measurement. A minimum of three trees were selected for each species so that the measured trees provided a good coverage of both size and age classes. In total, 20 sap flow meters were installed into 19 selected trees (Figure 1 and Table 1): 18 single trunk individuals and a double trunk *Melaleuca dealbata*. During tree selection, it was determined that there were some spatial trends in the locations of different species at this site. In particular, the *Melaleuca dealbata* were found within 8 m of the high-water mark for the adjacent lagoon, whereas the *Pandanus cookii* were found further away from the lagoon, with monitored trees occurring between 22 and 40 m from the high-water mark. The *Eucalyptus tessellaris* and *Acacia salicina* were spread throughout the riparian zone, occurring between 5 and 47 m and between 3 and 45 m, respectively, from the high-water mark. The initial DBH, distance from the lagoon, average measured sap flow rate and average sap flow velocity for each of these individual trees is presented in Table 1.

3.3. Tree Water Use

The heat ratio method (HRM) [26] was used to measure tree water use for a range of species. The HRM is a modification of the compensation heat pulse method [27], offering improvements by allowing for the measurement of both very slow flow rates and reverse sap flow. Measurements were made with ICT International SFM1 sap flow meters that make use of a thermometric method of measuring sap flow in xylem tissue using a short pulse of heat as a tracer. The HRM sensor consists of three 35 mm long needles that are connected to a 16-bit microprocessor; the central needle is a line heater that delivers a uniform heat pulse into the surrounding sapwood. The top and bottom needles contain two thermistors located at 7.5 mm and 22.5 mm from the tip. Measurement of the ratio of heat reaching each symmetrically placed outer needle allows for the direction and flow rate of water to be determined within the sapwood. Heat pulse velocity (V_h , cm/s) is calculated using Equation (1) [28]:

$$V_{h} = \frac{k}{x} \ln\left(\frac{v_{1}}{v_{2}}\right) 3600 \tag{1}$$

where k (cm²/s) is the thermal diffusivity of the fresh sapwood, x (cm) is the distance between the heater and either temperature probe (0.6 cm) and v_1 and v_2 are the increases in temperature at the equidistant points downstream and upstream from the heater.

The sapwood depth was measured by using an increment corer. Once the core had been carefully removed from the selected tree, methyl orange was used to stain each wood type a different shade, which increased the distinction between the sapwood and heartwood.

The sap flow meters were installed at a height of approximately 1.3 m and were set to take initial readings to ensure correct installation and initiation. Sap flow meters were then set to take a reading every 15 min. Preliminary data showed that the heat pulse for the sap flow meters installed in Eucalypt trees needed to be increased as a result of direct sunlight and the thermal properties of the wood. After this minor adjustment, the sensors were left to take recordings for a number of months, while fortnightly data downloads were undertaken to ensure smooth operation.

Species	Eucalyptus tessellaris					Melaleuca dealbata						Acacia	salicina	Pandanus cookii				
Plant ID	E1	E3	E4	E5	E6	M1	M2a	M2b	M3	A1	A2	A3	A4	A5	A6	P1	P4	P5
Diameter (cm)	12.0	42.5	29.13	16.2	36.61	13.37	49.02	41.06	43.0	20.37	6.53	9.39	5.73	15.60	5.73	13.37	15.6	17.19
Circumference (cm)	37.7	133.5	91.5	51	115	42	154	129	135	64	20.5	29.5	18	49	18	42	49	54
Distance from lagoon (m)	18.7	5.0	24.4	17.1	46.7	7.8	6.1	6.1	6.1	2.5	9.8	31.4	35.1	46.0	15.7	39.67	22.2	32.4
Xylem Radius (cm)	6.0	21.25	14.56	8.1	18.3	6.68	24.51	20.53	21.49	10.19	3.26	4.7	2.86	7.80	2.86	6.68	7.8	8.59
Sapwood Depth (cm)	3.5	2.2	2.5	3.5	4.0	2.25	2.5	2.0	2.0	2.5	2.0	2.0	2.0	4.0	2.0	6.68	7.8	8.59
Thermal Diffusivity (cm ² s ⁻¹)	0.0025	0.0025	0.0025	0.0025	0.0025	0.0025	0.0025	0.0025	0.0025	0.00258	0.00258	0.00258	0.00258	0.00258	0.00258	0.00201	0.00201	0.00201
Wound Diameter (cm)	0.22	0.22	0.22	0.22	0.22	0.23	0.23	0.23	0.23	0.21	0.21	0.21	0.21	0.21	0.21	0.20	0.20	0.20

Table 1. Characteristics of the monitored trees a	and sap flow rates for each tree.
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Data analysis and corrections were undertaken through the use of ICT's Sap flow Tool (v1.2; ICT International, Armidale, NSW, Australia). In this manner, sap velocity (V_s, cm/hr), and sap flow rate (Q, cm³/hr) were calculated from the raw heat pulse velocity (V_h, cm/hr). The majority of the parameters used for calculations with the Sap flow Tool are provided in Table 1. The remaining parameters, bark thickness, sap flow fresh weight, sap flow dry weight, and sapwood fresh volume were kept constant for all four tree species. It is recognized that these assumed parameters influence the accuracy of the sap flow measurements.

Sap velocity is calculated on an area basis by quantifying the fractions of sap and wood in the xylem and accounting for the difference in densities and specific heat capacities. This is because only a fraction of the xylem is made up of moving sap. Barrett et al. [29] formulated Equation (2) to calculate sap velocity (V_s):

$$V_{s} = \frac{V_{c}\rho_{b}(c_{w} + m_{c}c_{s})}{\rho_{s}c_{s}}$$
(2)

where V_c is the corrected heat pulse velocity (m/s), ρ_b is the density of wood (dry weight/green volume), ρ_s is the density of water (kg/m³), c_w and c_s are the specific heat capacity of the wood matrix (1200 J/kg/°C at 20 °C) [30] and sap (water, 4182 J/kg/°C at 20 °C) and m_c is the sapwood water content.

Sap flow rate is then determined by multiplying the sap velocity (V_s) by the crosssectional area of the conducting sapwood. As the sap velocity is estimated at two depths, the total sapwood area is divided into concentric regions separated by the midpoint between depths. There is then an option for how to treat the region beyond the last thermistor: hold value or linear decrease. Monocot stems, like that of the *Pandanus cookii*, are made up of vascular bundles spread across the entire cross-sectional area of the stem, whereas dicot stems are normally woody and contain a dry non-conducting core. For this reason, the option to hold the value was used for the monocot species (*Pandanus cookii*), while the linear decrease option was used for the remaining dicot species.

A key feature of the *Pandanus cookii* that was expected to influence sap flow rate estimates is that the entire cross-section of the *Pandanus cookii* stem comprises active conducting tissue (sapwood). Therefore, the entire radius was also used as the sapwood depth. In this manner, a whole of tree sap flow rate was determined for each of the *Pandanus cookii* trees under investigation.

Thermal diffusivity properties of the wood, sapwood fresh weight, sapwood dry weight, and sapwood fresh volume were determined from values obtained from the literature [28]. *Pandanus cookii* thermal diffusivity and wound diameter values were obtained from the work of Madurapperuma, Bleby and Burgess [24]. The *Acacia salicina* wound diameter estimate was obtained from Gwenzi et al. [31], while the thermal diffusivity value for the *Acacia salicina* trees was obtained from Forster [32]. The *Eucalyptus tessellaris* wound diameter was found in the work of Hatton, Moore, and Reece [21]. The approximated wound diameter for the *Melaleuca dealbata* trees was determined using the methodology of McJannet [22], whereby the diameter is assumed to be equal to the needle width plus one vessel width (0.5 mm) on either side. The default thermal diffusivity value of 2.5×10 – $3 \text{ cm}^2/\text{s}$ [28] was then used for both the *Eucalyptus tessellaris* and *Melaleuca dealbata* calculations.

3.4. Soil Moisture

A detailed record of soil moisture was required to correlate plant water usage with soil moisture levels to determine whether the monitored trees were tapping into the ground-water or making use solely of unsaturated zone water. Soil moisture monitoring locations were selected at five points evenly spaced along a transect running perpendicular to the wetland (Figure 1). Each monitoring location consisted of two transducer tensiometers and two moisture pressure sensors ([MPS]-1 sensors [ICT International]) that indirectly measure soil water potential. The tensiometers have an operating range of 0 to -100 kPa

while the MPS-1 sensor can operate at a range of -10 to -500 kPa. Two 30 cm and 60 cm holes were excavated at each location using a handheld auger, and a tensiometer and MPS sensor were inserted into pairs of holes at each depth. Care was taken to retain the original soil profile after excavation, as each hole was carefully backfilled to ensure the final soil profile properties, including horizon thicknesses and compaction characteristics, were approximately equivalent to the soil properties prior to excavating the holes.

3.5. Tree Growth

Stem growth was measured to allow for whole tree water relations to be determined. Logging band dendrometers (DRL26; ICT International) were installed on 10 selected trees across the study site (E1, E3, E5, M1, M2a, M2b, M3, P1, P4 and P5) to continuously log tree diameter at a height of 1.3 m (diameter at breast height [DBH]). Data logging at 30 min intervals provides information on diurnal stem fluctuations in response to climatic and micro-environmental effects in addition to long-term growth.

3.6. Groundwater and Surface Water

Knowledge of groundwater levels at the site is important to determine whether the ecosystem is groundwater dependent and, if so, to what extent. Two bore transects, each consisting of three bores, were drilled to 4–6 m depth, at either end of the riparian strip under investigation. Strata logs were recorded for each bore. Pressure transducers (In situ TrollTM) were installed below the water table in each bore to measure groundwater levels at 15 min intervals. A single barometric pressure transducer (In situ TrollTM) was installed in one of the bores to allow the groundwater level measurements to be corrected for barometric effects.

One pressure transducer was deployed for monitoring water levels in the lagoon. This pressure transducer was suspended from a bridge into the lagoon approximately 1.2 km upstream from the field site. To investigate the influence of the distance of monitored trees from the lagoon water on sap flow rates, the distances between the individual trees monitored, and the high-water mark of the lagoon were measured. However, the actual distance to the water in the lagoon was typically another 35 m further away than the high-water mark.

3.7. Data Analyses

The sap flow rates for all of the trees monitored were initially evaluated qualitatively. To illustrate the observed differences between the four species monitored and provide visual examples of the diurnal trends, a quadrant in the north-east corner of the monitoring site was selected that contained at least one replicate of each species in relatively close proximity to each other. The data for the each of these species were then plotted alongside the groundwater levels for the bore closest to these four trees. Linear regressions were used to explore relationships between sap flow and the vapor pressure deficit. Boxplots were used to present the variability in sap flow rates for each of the trees monitored before further statistical analyses, random forest modeling and principal components analysis, was completed.

To identify the variables that influence sap flow, we implemented two non-parametric models: random forest and principal components analysis (PCA). A random forest is a non-parametric ensemble of trees method, which uses a bagging algorithm to take bootstrap samples of training data, randomly selecting variables and constructing many individual decision trees in order to make predictions [33]. As a non-parametric model, the random forest is not constrained by statistical assumptions and there are no coefficients or betas produced by the model as in some traditional methods such as generalized linear models. Random forest models can identify variables that are most important to predicting an outcome as measured by a metric called variable importance (VI) [34]. Some examples include using variable importance to identify genes associated with particular diseases [35,36] in epidemiology and in ecology to identify stream conditions [37]. A key

benefit of using random forest models to identify important variables, also referred to as variable selection, is they can assess the multivariate interactions between multiple independent variables in addition to the effect of an individual independent variable on the dependent variable [38].

In order to use random forest models, any missing values need to be excluded from the analysis. We exclude the rainfall variable because the majority of values are missing. Additionally, after excluding other missing values across all remaining variables in the dataset the initial 102,266 observations were reduced to 65,409 observations. This still provides a substantial amount of data from training and testing the random forest models.

We split the 65,409 observations into two samples: 80% for training and 20% for testing for the random forest model following machine learning literature best practice. The training process involves 'learning' which variables are important for making predictions of the dependent variable based on the training set which includes predictor variables and values of the dependent variable. Once the random forest has learned from the training data, it is used to make predictions for the dependent variable on the testing set, which is foreign to the trained model. We fit random forest models using the randomForest package in the software R [39].

We ran five random forest models with different seed values to explore which variables would be identified as most important to predict sap flow. Five models were sufficient because the pattern of variable importance was consistent, and the model error as measured by root mean squared error (RMSE) was low.

We include the following variables in the random forest models: Sap flow as predicted by Distance from surface water, Species, Solar Radiation, Vapour Pressure Deficit, Depth to groundwater at the closest bore, Relative Humidity, Temperature, HOUR and MONTH. The model then identifies the relative importance of each variable in this set for accurately predicting sap flow.

PCA is a multivariate technique used to reduce the dimensionality of large datasets by generating a smaller set of summary indices that can be more easily visualized and analyzed [40]. The technique is able to highlight variations and bring out any strong patterns in a dataset by generating new variables called principal components that are linear combinations of the initial variables. PCA puts the maximum possible information into the first component so that principal component 1 (PC1) describes the parameters that result in the largest variation with the minimum error. PC2 lies perpendicular to PC1 and accounts for the next highest variations in the data. There are as many principal components as there are parameters. However, if the first two or three components capture most of the variability then the remainder can be ignored without losing important information.

To investigate relationships between sap flow and the other variables measured, we in addition to random forest we also applied a Principal Component Analysis (PCA) to the data set using R.-2.1.3 and the R package prcomp. For the PCA, the same initial processing was carried out on the dataset as for the random forest models. The following variables were included in the PCA: sap flow, distance from surface water, temperature, solar radiation, relative humidity, vapor pressure deficit, depth to groundwater at the closest bore, month, and hour. The data were scaled to have unit variance as part of the prcomp analysis.

4. Results

4.1. Soil Water Trends

The MPS-1 sensors that were installed at 30 cm depth suggested that the soil remained relatively dry (<–200 kPa soil moisture) during the dry season until late November. However, the soil saturated rapidly following the start of the wet season, with 139 mm of rainfall falling during January 2012. In contrast, the soil sensors that were installed at 60 cm depth indicated that the soil remained dry (<–500 kPa soil moisture) throughout both dry and wet seasons (from early August 2011 to late January 2012). As a result of these dry soil conditions, the tensiometers installed next to the MPS-1 sensors were not able to produce reliable results.

4.2. Groundwater Level Trends

Groundwater levels in the six bores drilled on the site ranged from 0.5 to 3.6 m below the ground surface. The groundwater levels responded rapidly to both rainfall and irrigation events (Figure 2).



Figure 2. Depth to groundwater for the six bores at the site, versus rainfall, with the timing of irrigation events on the neighboring property depicted by solid grey vertical lines in September and October.

Diurnal fluctuations were present for the water levels in all six bores, but these diurnal signals varied during the monitoring period. Throughout September 2011, two peaks in groundwater levels were clearly visible within each 24 h period (Figure 3). The amplitude of the morning peak was approximately double the amplitude of the afternoon peak. The timing of the afternoon peak roughly coincided with a peak in lagoon water levels further upstream. While daily surface water fluctuation at the site was around 0.01 m, the daily groundwater fluctuation was almost 0.02 m.

By November, the lagoon levels had become fairly constant and the diurnal fluctuation in groundwater had changed to just one peak per day in the early hours of the morning (Figure 4). These trends continued until the end of the surface water monitoring period in January 2012. The timing and amplitude of the diurnal fluctuations were almost identical for all the monitored bores, despite differences in the distance of each of these bores from the lagoon.



Figure 3. Diurnal fluctuations in sap flow for 4 of the trees monitored vapor pressure deficit and depth to groundwater in September 2011.

4.3. Sap flow Rates

Using the heat pulse data, sap flow rates were calculated for the four different tree species, which enabled comparisons to be made between these species. The *Melaleuca dealbata* and *Eucalyptus tessellaris* trees exhibited very high variability in hourly sap flow rates between 'replicates' (Figure 5). The *Eucalyptus tessellaris* trees were found to have the highest average daily sap flow rates (27,400 cm³/day), followed by the *Melaleuca dealbata* trees (19,200 cm³/day), *Pandanus cookii* (13,100 cm³/day), and *Acacia salicina* (7000 cm³/day). As a result of the large number of *Acacia salicina* trees at the Inkerman site, the contribution of transpiration by *Acacia salicina* trees to total transpiration at this site is expected to be significant, despite the lower average sap flow rate per tree.



Figure 4. Diurnal fluctuations in sap flow for 4 of the trees monitored, vapor pressure deficit and depth to groundwater in November 2011.

Overall, there was a steep increase in sap flow for all species once VPD increased from 0 to 1 kPa, and maximum sap flow rates were typically observed when the VPD was >2 kPa. Maximum sap flow rates typically occurred when solar radiation was greater than approximately 500 W/m² and when the relative humidity was <50%. However, peak sap flow rates were different for each tree species.



Figure 5. Boxplots showing the range of sap flow rates (with the 25th percentile, median and 75th percentile indicated by the rectangular box and potential outliers indicated with dots) for each of the individual trees monitored.

4.4. Diurnal Trends and Nocturnal Sap flow

The sap flow rates for all four of the species monitored showed clear diurnal patterns characterized by rapid early morning rises in transpiration and afternoon declines (Figures 3 and 4). One of the main differences between the diurnal trends for the four species relates to the change in sap flow rates during the day, which was typically higher for the *Eucalyptus tessellaris*, *Melaleuca dealbata*, and *Pandanus cookii* species than for the *Acacia salicina* species. The daily peaks for *Pandanus cookii* are the sharpest of any of the monitored species (Figures 3, 4 and 6).

Another key difference in the diurnal trends between species was the rates of nighttime sap flow. For *Eucalyptus tessellaris* nighttime sap flow occurred consistently throughout the monitoring period, at rates averaging 430 cm³/hr, 520 cm³/hr, 705 cm³/hr, 371 cm³/hr, and 2263 cm³/hr for E1, E3, E4, E5, and E6, respectively. These rates are 25–47% of the day-time rates averaging 914 cm³/hr, 2092 cm³/hr, 1663 cm³/hr, 789 cm³/hr, and 5386 cm³/hr for E1, E3, E4, E5 and E6, respectively. When VPD remained high at night relatively high night-time sap flow rates were maintained (Figure 3), but when VPD was observed to decline during the night in November, nighttime sap flow rates declined slightly during the night (Figure 4).

The initial DBH for the four *Eucalyptus tessellaris* trees monitored ranged from 12 cm (for E1) to 36.6 cm (for E6). For the *Eucalyptus tessellaris* trees, tree circumference typically increased at night and decreased during the day. In addition, tree circumference was found to increase rapidly following rainfall and following irrigation in September (Figure 6).



Figure 6. Diurnal variations in sap flow vs. DBH for 3 of the trees monitored, in September 2011 (left hand side) and November 2011 (right hand side).

For *Melaleuca dealbata*, nighttime sap flow rates declined during the night. The timing of nocturnal declines in sap flow rates for *Melaleuca dealbata* followed the timing of declines in VPD trends more closely than the other three monitored species (Figures 3 and 4). For some of the *Melaleuca dealbata* trees monitored in this study, M1 and M2A, there was a particularly strong correlation using a linear regression between nighttime sap flow rate and nighttime VPD, with R² of 0.88 and 0.54, respectively and *p* values of <0.01. Yet, for M2B and M3, the correlation between nocturnal sap flow and VPD was much lower, with R2 of 0.02 and 0.30 and *p* values of <0.01. Some discrepancies were noted in the *Melaleuca dealbata* sap flow data though as for M2A, nighttime sap flow was 57% of day-time sap flow rates but for M1A, installed on a different stem of the same tree, nighttime sap flow was greater than day-time sap flow (Table 2).

Species		Eucalyptus tessellaris					lelaleuca	dealba	ta		Acacia salicina						Pandanus cookii			
Plant ID	E1	E3	E4	E5	E6	M1	M2a	M2b	M3	A1	A2	A3	A4	A5	A6	P1	P4	P5		
Mean sap flow velocity (cm/hr)	102	65	69	38	194	5.7	85	4.1	25	103	71	56	106	55	16	68	47	85		
Mean sap flow rate (cm ³ /day)		28,907	19,382	5732	73,649	16,410	44,211	1852	14,448	724	3934	4329	4330	10,015	18,998	9986	9445	20,570		
S.D. for sap flow rate (cm ³ /hr)	345	1220	673	268	2117	424	1243	30	284	548	145	143	105	440	33	435	424	939		
Mean daytime sap flow rate (cm ³ /hr)		2092	1663	789	5386	1028	4626	140	632	1188	310	294	243	1457	109	738	833	2491		
S.D. for daytime sap flow rate (cm^3/hr)		1214	625	227	1777	298	851	36	274	358	129	103	66	404	33	400	367	843		
Mean nighttime sap flow rate (cm ³ /hr)		520	705	371	2263	311	2640	150	288	165	125	62	64	948	62	94	177	1085		
S.D. for nighttime sap flow rate (cm ³ /hr)	94	503	240	66	964	95	624	21	164	238	89	60	75	309	6	102	95	257		
Nighttime rate as percentage of daytime rate	47	25	42	47	30	30	57	107	46	14	40	21	26	65	13	13	21	44		

Table 2. Sap flow rates for each tree.

The initial DBH for the four *Melaleuca dealbata* trees monitored ranged from 13.4 cm (for M1) to 49.0 cm (for M2A). For M3, in September, expansion occurred during the night, but in November, expansion predominantly occurred between 6 am and 2 pm. Stem contractions for M3 also occurred rapidly in November, between the hours of 2 am and 6 am (Figure 6).

Nighttime sap flow rates for *Pandanus cookii* remained low for P1 and P4, averaging 94 cm³/hr and 177 cm³/hr, respectively. However, higher nighttime sap flow rates occurred for P5, averaging 1085 cm³/hr. Nocturnal sap flow rates for *Pandanus cookii* were 13–44% of daytime sap flow rates (Table 1).

The initial DBH for the three *Pandanus cookii* trees monitored ranged from 13.4 cm (for P1) to 17.2 cm (for P5). For P4, lower nighttime sap flow rates in September typically coincided with contractions of the trunk, and daily increases in tree circumference for P4 coincided with daily increases in sap flow rates (Figure 6). However, these trends deviated in November.

Nighttime sap flow rates for *Acacia salicina* were typically the lowest out of the four species monitored, with average nighttime sap flow rates ranging from 62 to 64 cm³/hr for A3, A4, and A6. However, A1, A2, and A5 exhibited higher nighttime sap flow rates, averaging 165 cm³/hr, 125 cm³/hr, and 948 cm³/hr, respectively. For the *Acacia salicina* trees, nocturnal sap flow rates ranged from 14% to 65% of daytime sap flow rates (Table 1). The highest nighttime sap flow rates occurred for the *Acacia salicina* tree with the greatest initial DBH, while the lowest nighttime sap flow rates occurred for the *Acacia salicina* with the smallest initial DBH.

4.5. Sap flow Variations with Depth to Groundwater

Sap flow variations during a period of declining groundwater levels, from September to December 2011, were examined. For two of the *Eucalyptus tessellaris* trees monitored (E1 and E4), reductions in sap flow rates coincided with declining groundwater levels from September to December. For one of the *Eucalyptus tessellaris* trees (E4), which was located approximately 24 m from the lagoon, reductions in sap flow rates occurred once depths to groundwater exceeded 0.8 m. However, for one of the other *Eucalyptus tessellaris* trees (E1), which was located approximately 19 m from the lagoon, small and large reductions in sap flow rates occurred at 1.1 m and 1.2 m, respectively (Figure 7). The reductions in sap flow rates were first observed in the outer sensor from mid-October to late December, and in January, with both the inner and outer sensors displayed declining sap flow rates. Sap flow rates for E1 and E4 only began to increase again in the second half of January 2012 following a heavy rainfall event of 65 mm over five days, which resulted in a rise in groundwater levels of approximately 0.2 m.

For E6, sap flow rates reduced from 4600 cm³/hr to 2000 cm³/hr in early January 2012, when groundwater levels dropped to below 2.3 meters (Figure 7). In the second half of January, sap flow rates recovered as groundwater levels rose. E3 displayed a small decline in sap flow as groundwater levels declined, with sap flow just declining for two days in December 2011, then increasing. E5 displayed no decline in sap flow as groundwater levels declined.

Steady decreases in sap flow rates (from 518 cm³/hr to 364 cm³/hr) for *Pandanus cookii* tree P1 did occur in response to increasing depths to the groundwater table but only once groundwater dropped from 2.30 to 2.35 m below ground level. The other *Pandanus cookii* trees and the *Acacia salicina* and *Melaleuca dealbata* trees monitored did not exhibit drops in sap flow when groundwater levels declined.





Figure 7. Depth to groundwater vs. average hourly sap flow rate for each day for the three *Eucalypus tessellaris* trees that exhibited declining sap flow rates during the period of declining groundwater in late November and early December 2011.

4.6. Which Factors Are Most Important in Influencing Sap Flow?

The results from principal component analysis of the whole dataset indicated that 60% of the variability in the dataset was explained by PC1 and PC2. PC1 was primarily driven by climatic variables: temp, solar radiation, relative humidity, and vapor pressure deficit and PC2 was primarily driven by groundwater level, distance to surface water and sap flow (Figure 8). Hour and month did not contribute significantly to either PC1 or PC2. The fact that groundwater level, distance to surface water and sap flow all contribute to PC2 provides supporting evidence that there is a correlation between sap flow and these 2 hydrological factors. The fact that sap flow is also heading in the direction of PC1 indicates that, as expected, climatic variables are also important in influencing sap flow.

The results of the principal component analysis also provide supporting evidence that there is more difference between individual trees than between species. However, the *Melaleuca dealbata* trees typically plotted lower, and in a tighter cluster, than the other species (Figure 9). The *Melaleuca dealbata* trees were all growing close to the lagoon, where groundwater was closest to the surface. All other species monitored were located a range of distances from the lagoon.

The random forest modeling provided further insights into the factors influencing sap flow. Figure 10 shows the relative importance of variables for predicting sap flow, from most important at the top right of the plot to least important at the bottom left of the plot for one of the random forest models. This model had RMSE = 5.833. Distance from the lagoon was consistently the most important variable for predicting sap flow across all the random forest models. This was followed in importance by the depth to groundwater, species, solar radiation, VPD, relative humidity, temperature, hour of the day, and month of the year.



Figure 8. Score plot from the PCA, showing that PC1 was driven by the climatic variables and PC2 was driven by hydrologic variables (distance from the lagoon and depth to groundwater).



Figure 9. Score plot from the PCA, showing the influence of species and variability between individual trees on the PCA results.



Figure 10. Random forest variable selection results for one of the five random forest models. Variables are plotted from most important in predicting sap flow (top right of panel) to least important in predicting sap flow.

5. Discussion

Published sap flow measurements were not available for the exact species investigated at this field site. However, some of the sap flow trends observed for *Eucalyptus tessellaris* and *Melaleuca dealbata* were similar to closely related species.

Phreatophytic plants have previously been found to draw proportionally more water from greater depths using sinker roots as soil water becomes less abundant [41]. In this study, the reductions in sap flow rates that occurred for the *Eucalyptus tessellaris* when groundwater levels receded were particularly noticeable for the outer sensor. Prior research has attributed this to reductions in flow via superficial roots [42]. In contrast, the sap flow rates for the inner sensor, attributable to flow via sinker roots [42], remained fairly stable during the same period. This is consistent with previous results for *Eucalyptus canaldulensis*, showing that this species is highly opportunistic, accessing groundwater when it is available [43].

A strong correlation between sap flow rates and VPD has also been reported in previous studies for other Melaleuca spp, such as *Melaleuca quinquenervia* [22]. Yu et al. [44] determined that a weak correlation between sap flow and VPD indicates that the nocturnal sap flow should be attributed to both nocturnal transpiration and hydraulic redistribution, whereas a strong correlation between nocturnal sap flow and VPD indicates that the nocturnal sap flow can be attributed primarily to nocturnal transpiration. Therefore, for some of the *Melaleuca dealbata* trees monitored in this study, with strong correlations between sap flow can be attributed primarily to nocturnal transpiration. For the remaining *Melaleuca dealbata* trees, the correlation between nocturnal sap flow and VPD was much lower, indicating that nocturnal sap flow in these trees was a mixture of hydraulic redistribution and nocturnal sap flow.

Significant differences were found between the findings from the only monocot monitored in this study, *Pandanus cookii*, and the results reported by Madurapperuma, Bleby and Burgess [24] for cultivated palms, *Syagrus romanzoffiana*. In this study, the *Pandanus cookii* trees exhibited sharp daily peaks in sap flow (i.e., the maximum sap flow rate was almost the same each day despite changes in the maximum VPD). However, the only previous study of sap flow rates for 'woody monocots' by Madurapperuma, Bleby and Burgess [24,30] found the sap flow responses to be very dynamic and sensitive to changes in soil moisture and tree age. One possible explanation for these contrasting findings is the presence of shallow groundwater levels in the Lower Burdekin, providing more constant access to water for the *Pandanus cookii* trees.

5.1. Evidence of Groundwater Dependence

At the riparian field site, groundwater levels were typically close to the surface. Therefore, groundwater is expected to be accessible by most, if not all, trees at the site. Strong relationships between depth to groundwater level and sap flow are expected to occur as a result of the effects of transpiration by the mixed stand at the site potentially lowering the groundwater table. Analysis of the correlation between diurnal groundwater level signals and diurnal sap flow signals showed that groundwater levels clearly showed a recovery phase when sap flow rates reduced at night. However, the diurnal groundwater level signal exhibited two cycles of drawdown and recovery within each 24 h period during September (Figure 3). This pattern in groundwater levels could be explained by the superimposed effect of different species with different diurnal effects on groundwater levels. However, correlations between the timing of groundwater fluctuations and the timing of fluctuations in the nearby lagoon indicate that local groundwater–surface water interactions might also be contributing to the double diurnal signals. Although the lagoon at the field site was not directly connected to tidal waters, the proximity to the coastline may result in some tidal influence on the lagoon. As noted by Butler et al. [7], water table fluctuations are the integrated response to a group of highly heterogeneous stresses, including plant water use, vegetation characteristics, and aquifer characteristics.

While the diurnal fluctuations in groundwater levels provide supporting evidence that the trees are accessing groundwater, the 'double fluctuation' in groundwater levels observed for some of the monitoring period made it difficult to use the groundwater level measurements alone to estimate ET rates at this site. Moreover, if the groundwater level fluctuation method [5] were to be applied at this site, the occurrence of nighttime sap flow for some of the species would need to be considered. The dry soil conditions in the unsaturated zone further highlight the likely use of groundwater by the trees to meet water requirements. Therefore, the species that showed consistently high-water uptake throughout the year would likely have roots deep enough to access shallow groundwater.

Monitoring at this riparian field site identified different relationships between groundwater levels and sap flow depending on species. *Acacia salicina* and *Melaleuca dealbata* did not exhibit drops in transpiration when groundwater levels declined, which suggests that the trees monitored are not limited to accessing soil water and are readily accessing groundwater even when groundwater levels decline. For the *Acacia salicina* trees, this indicates that the roots are sufficiently deep to access groundwater to depths of up to 2.4 m. The occurrence of stable daily sap flow rates for the *Melaleuca dealbata* trees throughout the monitoring period can be explained by two factors. First, Melaleuca species have previously been found to have dynamic root systems that can quickly respond to rising and falling water tables [22]. In addition, the location of these trees along the lagoon boundary means that groundwater is always shallower (i.e., within 1.3 m of the ground surface).

Pandanus cookii only exhibited slight drops in sap flow rates when the depth to groundwater increased to more than 2.3 m. The consistently high sap flow rates across the rest of the monitoring period indicate that the *Pandanus cookii* are not limited by soil water availability. Therefore, the *Pandanus cookii* must have roots in constant contact with groundwater. Based on the depth to groundwater where these three monitored *Pandanus cookii* trees were located, their roots must penetrate to at least a depth of 2.3 m. The *Eucalyptus tessellaris* exhibited different results. Following long-term dry conditions, sap flow rates for both the inner and outer sensors reduced. The reduction in sap flow rates for two of the *Eucalyptus tessellaris* trees (E1 and E4) when groundwater levels dropped indicates that most roots for these *Eucalyptus tessellaris* trees at this site only penetrate to a depth of approximately 1.2 m below the ground surface. Yet, for E6, sap flow rates did not decline until groundwater was approximately 2.3 m below the ground surface.

The investigation of relationships between depth to groundwater and sap flow was hampered by the short monitoring period included in this study, which only extended from the end of one dry season to the middle of the following wet season (from early August 2011 to late January 2012). This means that the full impact of the wet season was not able to be investigated. Monitoring periods of at least 12 months are recommended for future studies.

5.2. Is Depth to Groundwater a Strong Predictor of Sap Flow Rates?

Both the random forest model and the PCA results indicated that depth to groundwater was an important variable in influencing sap flow. Therefore, the application of these methods provided evidence that sap flow rates were strongly influenced by depth to groundwater at this site.

The differences in responses between species present challenges when modeling relationships between ET and depth to groundwater for this mixed stand. For the species that exhibited changes in sap flow with declines in groundwater levels, representative transpiration rates could be derived for the observed range of depths to groundwater. Based on the field monitoring data, we could potentially develop an 'ET curve', which depicts the relationship between depth to groundwater and sap flow rates, for *Eucalyptus tessellaris*. However, significant variability was observed between individual trees. Therefore, 'upscaling' ET rate measurements and ET curves from individual trees becomes challenging. To date, it is not known whether the variability in sap flow rates between trees was due to hydrological differences (e.g., heterogeneity in soils and aquifer properties) or ecological differences between individual trees. Thus, it is critical that multiple replicates are included for each species when monitoring ET rates.

An important component of ET curves when considering water management is 'extinction depth'; that is, what are the critical depths to groundwater beyond which groundwater ET no longer occurs? This is particularly relevant for water management at the field site in the present study, as there have recently been changes in the local hydrology because of management practices that aim to improve wetland health by drying out the wetland at the riparian site.

Determining the appropriate 'extinction depths' can be challenging. As the root depth for phreatophytic trees can vary in response to groundwater accessibility [45], our ability to measure 'extinction depth' depends on groundwater levels declining past the depth for which these trees have developed root systems. For the *Melaleuca dealbata* trees in particular, an extinction depth would be purely hypothetical under natural conditions, because these trees will establish themselves in locations where groundwater tables are at accessible depths (Figure 1). As a result, an extinction depth would only occur in circumstances of rapid groundwater level depletion (e.g., in the event of over-extraction).

As there are distinct differences in sensitivity to groundwater levels between species at this site, it would not be appropriate to predict ET rates based solely on depth to groundwater. Longer-term monitoring of species at this site, combined with an extended monitoring area to cover a greater range of depths to groundwater, would be advisable before quantifying the relationships between depth to groundwater and ET rates for this 'mixed stand'. In addition, investigating rooting depths and using stable isotope techniques for source apportionment would provide complementary information to the results described in this paper.

5.3. Is Distance to Surface Water a Strong Predictor of Sap Flow Rates?

During the field monitoring period, September 2011-January 2012, the wetland did not drain seasonally. This is expected to have caused seasonal variations in the lagoon height to be diminished. As a result, it is expected that the lagoon would have been a constant potential water source for the riparian trees throughout the study period and the water in the lagoon is likely to have helped to maintain soil water levels in the hyporheic zone.

Distance to the lagoon was identified as the most important variable for explaining variation in sap flow, based on the random forest modeling (see Figure 10). The PCA results indicated that ecohydrological variables monitored showed lower variance for the *Melaleuca dealbata* trees than for the other tree species monitored (Figure 9). This trend may be caused by the location of the *Melaleuca dealbata*, close to the lagoon. The increased variance for the ecohydrological variables for the other species may be a result of their wider set of locations relative to the lagoon.

A previous study investigating the influence of distance from the river on groundwater transpiration rates found that groundwater drawdown because of transpiration decreased for bores closer to the river [19]. However, in the present study, the daily drawdown for the bores at the Inkerman riparian site did not decrease for bores closer to the lagoon. The difference in groundwater drawdown patterns may be partly due to differences in sediment type as the Johnson et al. (2013) [19] study focused on an aquifer rich in sand and gravel whereas the sediments at our study site were clay rich.

5.4. Methods

The heat ratio method that was applied in the field monitoring component of this study in 2011–2012 has recently been determined best suited for measuring sap flow where sap flow rates are low and recent progress has also been made in addressing errors introduced by probe misalignment, including potential errors in measurements of nocturnal sap flow [46]. In addition, it is recognized that the accuracy of the sap flow estimates analyzed in this study would have been impacted by the use of literature or assumed/default values for certain parameters needed for calculating sap flow rates, including bark thickness, sapwood fresh weight, sapwood dry weight, and sapwood volume. Despite these limitations, this study has still been able to provide some insights into the diurnal trends in sap flow, groundwater dependence of the species monitored and the application of random forest modeling to ecohydrological studies. Therefore, it is recommended that for future ecohydrological monitoring studies, the combination of a statistical technique such as random forest modeling with improved field measurements and corrections of probe misalignment will provide greater insights into the factors controlling sap flow rates.

In this study, we used PCA for a comparison with a random forest because it is a long established technique which has been used across many disciplines [40]. Although random forest has been used to identify variable importance in some ecological contexts, as described in Section 3.7, it is not yet commonplace in the field. Given this, it was appropriate to include PCA as a benchmark non-parametric method. In future studies there would be merit in exploring the use of a similar and relatively newer technique Projection of Latent Structures (PLS), which combines features of multiple linear regression and PCA [47].

6. Conclusions

The *Eucalyptus tessellaris* trees were found to have the highest average daily sap flow rates (27,400 cm³/day), followed by the *Melaleuca dealbata* trees (19,200 cm³/day), *Pandanus cookii* (13,100 cm³/day), and *Acacia salicina* (7000 cm³/day). However, both the inter-species and the intra-species variability in sap flow rates was high.

This study has demonstrated that combining ecohydrological monitoring, principal component analysis and random forest modeling was effective for determining the factors influencing sap flow at a riparian site. Species, depth to groundwater and distance from the lagoon were all found to be important in influencing sap flow rates. Random forest modeling results indicated that distance from the lagoon was the most important predictor

of sap flow, relative to the other variables considered, followed by depth to groundwater and species. Results from random forest and PCA modeling were consistent identifying important variables influencing sap flow.

This study has highlighted a number of challenges associated with using ecohydrological monitoring to inform ET estimation and ET curve development. These challenges are associated with the measured variability between species—and even between trees of the same species—regarding relationships between sap flow and depth to groundwater.

While strong diurnal signals were present in the sap flow data for all species, significant rates of nighttime transpiration were detected for *Melaleuca dealbata* and *Eucalyptus tessellaris*. For both of these species, nighttime sap flow rates were typically correlated with VPD.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to data sharing policies of the data owners.

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