

Groundwater use by dominant tree species in tropical remnant vegetation communities

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Abstract. Defining groundwater dependence and water-use requirements of terrestrial vegetation represents a significant challenge to water-resources managers. Terrestrial vegetation may exhibit complex spatial and temporal patterns of groundwater dependence. In this study we have assessed the sources of water used by dominant tree species in remnant vegetation of Pioneer Valley, Mackay, in northern Queensland. Water use by tree species was determined by sapflow techniques and the sources of water were investigated by using a combination of isotopic and water-potential measurements. Within the remnant vegetation communities of the Pioneer Valley there were complex patterns of water use and water-resource partitioning. However, all communities within the study showed some degree of groundwater use. Riparian communities that were reliant on groundwater discharge for maintenance of river baseflow exhibited high species diversity and complex forest structure and different species within these communities accessed a range of water sources including shallow soil water, river water and groundwater. In contrast, the woodlands and open forest were principally reliant on soil water. Although, species such as *Corymbia clarksoniana* appeared to be reliant on groundwater for their dry-season water-use requirements. This study demonstrated use of groundwater by remnant vegetation communities in the Pioneer Valley but determination of groundwater dependence requires a better understanding of the temporal patterns of water use and sources of water used by each species.

Introduction

Remnant terrestrial vegetation is being increasingly recognised as a valuable resource in heavily modified landscapes. Apart from being important for biodiversity (Moore and Renton 2002), remnant communities may play an important role in regional hydrology (Cramer and Hobbs 2002). Active management is required to protect remaining remnant and riparian vegetation and these communities may to varying degrees depend on uptake of groundwater, either to sustain transpiration and growth through a dry season or for the maintenance of perennially lush ecosystems in otherwise water-limited environments. Despite this, our understanding of the nature of groundwater dependence in terrestrial vegetation is limited (Hatton and Evans 1998).

Several methods are available for studying the water use and the sources of water used by terrestrial vegetation. Plant transpiration can be estimated by using water-balance techniques (Myers *et al.* 1996), eddy covariance methods, ventilated chambers (Hutley *et al.* 2000) or by sapflow

methods such as heat-pulse techniques (O'Grady *et al.* 1999). Sapflow methods have distinct advantages over other measures of tree water use in that they can be operated at a range of spatial and temporal scales and are easily automated (Smith and Allen 1996; Köstner *et al.* 1998; Wullschlegel *et al.* 1998). In addition, isotopic methods have been successfully used to differentiate water sources for plants with access to both ocean and freshwater (Sternberg and Swart 1987), stream water and soil water (Dawson and Ehleringer 1991), and soil water and groundwater (Zencich *et al.* 2002). The combination of sapflow and isotopic techniques therefore has the potential to quantify rates of water use from different sources. The results of these types of analysis, however, are sometimes ambiguous. Therefore, comparison of leaf water potential and soil water potentials may add further information on sources of water used by plants as it is often assumed that, in the absence of nocturnal transpiration, pre-dawn leaf water potential is in equilibrium with soil water potential in the zone of water uptake (Schulze and Hall 1982; Ritchie and Hinckley 1975).

Since the 1994 Council of Australian Governments framework for water reform, the allocation of groundwater resources for the maintenance of ecosystem processes has been a pressing issue (COAG 1996). The reform framework requires water-resource managers to account for, and allocate, water resources to maintain environmental flows and values. However, the extent and importance of groundwater-dependent ecosystems within Australia is poorly understood and demand for access to groundwater resources is increasing. In 2002, the Queensland Department of Natural Resources and Mines embarked on a major study of groundwater-dependent ecosystems in the Pioneer Valley, central Queensland. This information would then be used in development of the groundwater management plan for the region. This paper describes the investigation into groundwater use by remnant terrestrial vegetation in this region.

Materials and methods

Site description

The Pioneer Valley is a broad alluvial valley on the central Queensland coast (Fig. 1). The region has a subtropical weather pattern that features distinctive wet and dry seasons. Average annual rainfall ranges from ~1650 mm at the coast and in the ranges to the west to 1400 mm in the central areas of the valley. Typically, 80% of the annual rainfall occurs in the 6 months from November to April. The valley is bounded to the south, west and north by the Clark-Connors Range, which rises to an elevation of ~1200 m above mean sea level (a.m.s.l.) at its highest, but averages ~600 m a.m.s.l. and is drained by the Pioneer River, Sandy Creek, Bakers Creek and Alligator Creek.

Vegetation within the catchment has been extensively cleared, particularly for sugarcane production. Remnants within the catchment have been mapped and classified with respect to vegetation structure, condition and ecological status (Clear 2000; Werren 2001). Prior to clearing, much of the catchment was dominated by ironbark (*Eucalyptus crebra*) forests, woodlands comprising *Eucalyptus platyphylla*, *E. tereticornis*, *Corymbia intermedia*, *C. clarksoniana* and *Melaleuca* woodlands to open-forests dominated by *M. viridiflora*. Swamps, riparian rainforests and notophyll-microphyll vine forests also occur. Vegetation remnants within the catchment are highly fragmented and many show signs of extensive invasion by exotics (Werren 2001). However, they remain important refuges for biodiversity.

Four sites were identified as being potentially groundwater dependent on the basis of existing mapping, infrastructure (monitoring bores) and local knowledge. Sites are described in Table 1. All measurements were made between 17 August and 3 September 2003. Measurements were timed to coincide with the dry season, when groundwater use was likely to be at a maximum.

Vegetation assessment

At each site, transects or plots were established to characterise vegetation structure. Within each plot, species composition, diameter at 1.3 m (DBH), canopy condition and canopy cover were recorded. Canopy condition of individual trees was visually assessed and scored by using an ordinal scale (0–5). A canopy in excellent condition, defined as having no loss of small terminal branches was given a score of 5. Dead trees were given a score of 0. Within each plot or transect, replicate ($n = 3$) measures of canopy cover were made with a spherical densiometer (Lemon 1957). Depth to watertable at the site was measured in a nearby bore, and watertable depth for each tree was estimated by surveying surface elevations and assuming the watertable to be horizontal.

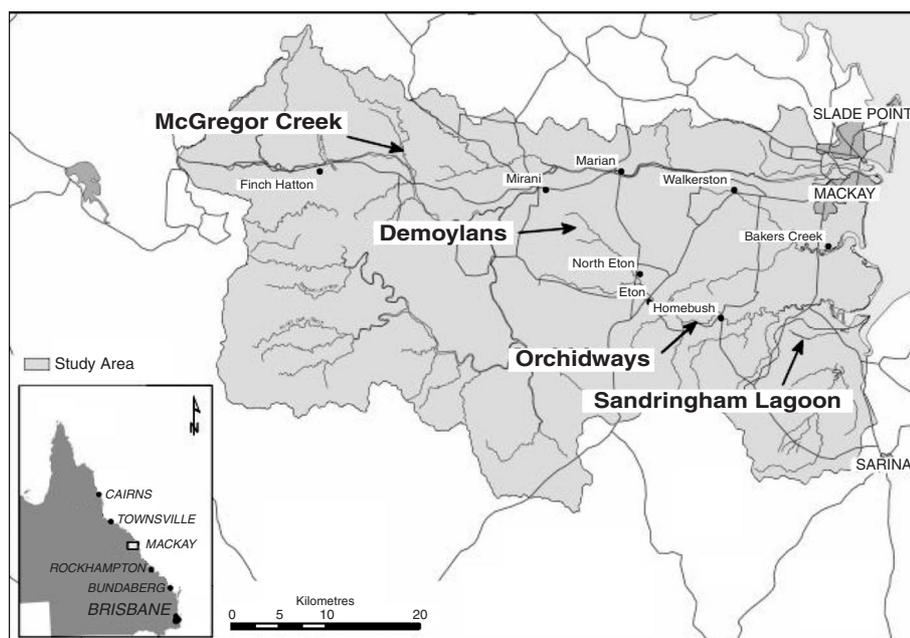


Fig. 1. Location map showing the location of the Pioneer Valley within northern Queensland as well as the four remnant vegetation communities examined in this study.

Table 1. Description of sites in the Pioneer Valley and depth to groundwater

For the two riparian sites a range of depth to groundwater is shown from the creek to the levee. Classification of potential groundwater-dependent ecosystem (GDE) type follows Hatton and Evans (1998)

Site	Description	Depth to watertable (m)	GDE type
Demoylans	<i>Eucalyptus platyphylla</i> – <i>Melaleuca viridiflora</i> woodland	10	Terrestrial/wetland
Sandringham Lagoon	<i>Corymbia tessellaris</i> – <i>Lophostemon suaveolens</i> – <i>M. viridiflora</i> woodland, with <i>M. leucadendra</i> fringing the lagoon	4	Terrestrial/stream baseflow
Orchidways on Sandy Creek	<i>M. leucadendra</i> riparian forest	0–10	Stream baseflow
McGregor Creek	Riparian mesophyll forest with feather palm and <i>Melaleuca</i>	0–10	Stream baseflow

Tree water use

The compensation heat-pulse technique was used for measurement of tree water use. Measurements were made with Greenspan sapflow loggers (Greenspan, Warwick, Qld). A 1.8-s heat pulse was fired at 15-min intervals. Heat-pulse velocity was measured at four depths within the sapwood to characterise radial profiles in sap velocity. Heat-pulse velocity was corrected for wounding by using the solutions of Swanson and Whitfield (1981), assuming a wound width of 3.1 mm (O'Grady 2000). Sap velocity was calculated following Edwards and Warwick (1984) and scaled to tree water use by using the weighted averages technique of Hatton *et al.* (1990). On each tree, DBH, bark thickness and depth of sapwood were measured. Sapwood depth was determined using an increment corer and heartwood–sapwood separation determined on the basis of a colour change or by using a di-methyl orange dye that differentially dyes heartwood and sapwood. Wood cores from each tree were stored in sealed vials and kept for measurements of wood density and water content. The number of trees and the species measured at each site varied. In general, water use was measured in up to 10 individual trees at each site. Trees were chosen to represent the dominant species in each community and to cover a range of tree sizes.

At each site one tree was randomly allocated as a reference tree. Water use of reference trees was measured over a 12-day period. A system of roving loggers was employed to measure the water use of the remaining sample trees. Each tree was instrumented and measured over a 2–3-day period and hourly fluxes were compared to the fluxes measured in the reference tree by using linear regression (Vertessy *et al.* 1997; Hunt and Beadle 1998), to account for large daily fluctuation in water use. However, day-to-day variability in transpiration was low (<15%); therefore, only actually measured water use is reported here.

Leaf and soil water potential

Pre-dawn leaf water potential was measured with a Scholander-type pressure bomb (PMS instrument Co., OR, USA). Measurements of leaf water potential were made on two leaves from each tree for which tree water use was being concurrently estimated. Leaves were cut and immediately placed in sealed humid bags and stored in a dark, insulated container until measurement, typically within 30 min of sampling. Donovan *et al.* (2001) highlighted the potential problem of pre-dawn disequilibrium between leaf water potential and soil matric potential. To assess this, leaf water potential was measured throughout

the morning at Sandringham Lagoon and Demoylans and a relationship established between leaf water potential and flow. These relationships were extrapolated to zero flow as an estimate of water potential at zero flow (Bucci *et al.* 2004).

Soil samples were collected by hand-auguring to depths of up to 8.5 m, with samples collected at ~0.5-m intervals, and placed in glass jars to minimise evaporation. Where the core reached the watertable, a measurement of the standing water level was made 24 h after completion of the hole, to allow sufficient time for water to enter the hole. Soil samples were analysed for gravimetric water content and matric potential. Gravimetric water content was measured by oven-drying a subsample at 105°C for 24 h. Soil matric potential was measured by using the filter paper technique (Greacen *et al.* 1989).

Isotopic composition

The ¹⁸O composition was determined for soil water, groundwater, surface water and xylem water (extracted from twig samples). Three twig samples of ~10-mm diameter were collected from the canopy of trees with pruning shears. These were stripped of bark, cut into 50-mm lengths, placed in glass jars and covered with kerosene before sealing with a screw-top lid. Plant material and soils were azeotropically distilled in kerosene, following the methodology of Revesz and Woods (1990) and Thorburn *et al.* (1993). Samples were analysed with a dual-inlet gas ratio mass spectrometer. Oxygen-18 was preferred to ²H because the analytical process is simpler. Isotopic concentrations were expressed as delta (δ) values per mille (‰) relative to the standard SMOW (standard mean ocean water). The mean difference between replicate twig samples was 0.43‰, and the median difference was 0.26‰. Differences indicate errors involved in extraction of soil water and analytical precision, but also possible differences in water sources of different roots (flow through the tree does not necessarily mix water obtained from different sources, extracted by roots at different depths). Analytical precision for ¹⁸O is ~0.15‰ (one standard deviation).

Results

Tree size, tree water use, leaf water potential, 'no-flow' water potential and xylem isotopic concentrations for all trees surveyed are shown in Table 2. Hourly fluxes (Q_s) have been normalised for tree size, and are presented in units of cubic metre of water per hour per square metre of sapwood area. $Q_{s\max}$ is the maximum hourly flux on a diurnal basis. Mean

Table 2. Tree size statistics, mean daily water use, pre-dawn leaf water potential and xylem ¹⁸O composition

Minimum daily xylem water potential is also included for trees on which xylem water potential was measured throughout the morning. Watertable depths were inferred from measurements on nearby observation bores

Site	Tree	DBH (mm)	Watertable depth (m)	Q (L day ⁻¹)	Q_{smax} (m ³ h ⁻¹ m ²)	Ψ_{pd} (MPa)	Estimated no-flow Ψ_{pd}	Minimum lwp (MPa)	¹⁸ O (‰)
DeMoylans Lagoon	<i>C. clarksoniana</i>	298	10.17	16.25	0.21				
	<i>C. clarksoniana</i>	132		21.38	0.37	-0.4	-0.18	-1.10	-4.05, -4.19
	<i>E. platyphylla</i>	163	10.24	14.91	0.25	-0.88	-0.56		-3.28
	<i>E. platyphylla</i>	168		24.34	0.24				
	<i>E. platyphylla</i>	423	9.69	74.28	0.44	-0.65	-0.38	-2.25	-2.83, -2.66
	<i>L. suaveolens</i>	151	10.25	7.92	0.11				-3.05
	<i>L. suaveolens</i>	108	10.18	5.72	0.15	-1.08	-0.73	-2.40	-3.18, -3.18
	<i>M. viridiflora</i>	72	10.24	3.65	0.17	-0.68	-0.40		-3.67, -3.38
	<i>M. viridiflora</i>	149	9.98	6.33	0.17	-0.81	-0.51	-1.75	-3.71, -1.77
	<i>M. viridiflora</i>	86	9.35	3.65	0.21	-0.58	-0.32		-3.74, -4.00
Sandringham Lagoon	<i>C. tessellaris</i>	85	4.63	6.02	0.23	-0.38	-0.16	-1.11	-2.34, -2.81
	<i>L. suaveolens</i>	204	4.66	7.47	0.22	-2.17	-1.56	-2.95	-1.91, -1.06
	<i>C. tessellaris</i>	102	4.66	15.69	0.27	-0.23	-0.05	-1.45	-2.49, -2.51
	<i>M. viridiflora</i>	135	4.12	21.47	0.37	-0.55	-0.30	-1.1	-2.15, -2.26
	(hybrid)								
	<i>C. tessellaris</i>	405	4.62	51.80	0.29	-0.34	-0.14		-2.53, -1.93
	<i>C. tessellaris</i>	98	5.29	20.69	0.57				
	<i>L. suaveolens</i>	45	4.66			-2.40	-1.80		0.35
	<i>M. viridiflora</i>	27	5.36			-0.73	-0.45		
	<i>M. viridiflora</i>		5.29			-1.1	-0.74		
McGregor Creek	<i>C. clarksoniana</i>	293	7.97	137.54	0.578	-0.03	0.0		-4.50
	<i>C. clarksoniana</i>	373	7.83	122.69	0.477				
	<i>E. platyphylla</i>	85	7.83	3.75	0.183	-0.38	-0.16		-3.93, -3.44
	<i>C. cunninghamiana</i>	187	0.39	34.37	0.263	-0.54	-0.07		-3.21, -3.09
	<i>C. hypospodia</i>	334	3.77	46.48	0.179	-0.33	-0.12		-3.71, -3.79
	<i>C. triplinervis</i>	251	5.49	10.76	0.209	-0.38	-0.16		-5.6, -3.58
	<i>L. suaveolens</i>	92	7.29	9.86	0.351	-0.40	-0.18		-2.94, -2.96
	<i>L. suaveolens</i>	310	7.51	90.15	0.375	-0.24	-0.05		-3.56, -3.24
	<i>L. suaveolens</i>	286	7.58	32.77	0.207	-0.30	-0.10		-3.63, -3.85
	<i>M. leucadendra</i>	128	7.31	9.14	0.155	-0.78	-0.48		-3.32
	<i>M. leucadendra</i>								-3.94
	Orchidways	<i>A. philippinensis</i>	153	4.41	32.36	0.658	-1.55	-1.10	
<i>C. viminalis</i>		156	3.49	0.75	0.031	-0.55	-0.30		-3.66, -3.62
<i>E. platyphylla</i>		344	14.34	108.46	0.589	-0.40	-0.18		-2.74, -3.61
<i>M. tanarius</i>		113	12.03	6.16	0.099	-0.55	-0.3		-2.11
<i>M. tanarius</i>		178	7.77	27.34	0.187	-0.23	-0.04		-3.85
<i>M. leucadendra</i>		354	6.18	44.85	0.275				-4.90
<i>M. leucadendra</i>		431	8.18	40.43	0.040				-5.85
<i>M. leucadendra</i>		888	1.23	206.10	0.248				-2.67
<i>M. leucadendra</i>		264	9.29	27.45	0.188				-6.68
<i>M. leucadendra</i>		352	2.94	54.47	0.279	-0.38	-0.16		-4.16, -4.01
<i>M. leucadendra</i>		554	0.71			-0.05	0.0		-3.57
<i>P. guajava</i>			4.04			-1.80	-1.31		

daily fluxes (Q) are presented in units of litres per day, and have not been normalised for tree size. Detailed results on a site-by-site basis are presented below.

There were strong relationships between pre-dawn leaf water potential and flow throughout the morning for trees at Demoylans and Sandringham lagoon. This relationship was

used to predict the 'no-flow' pre-dawn leaf water potential. Measured pre-dawn leaf water potential underestimated (was more negative than) the 'no-flow' leaf water potential but there was a strong relationship between measured pre-dawn leaf water potential and the calculated no-flow leaf water potential (Fig. 2).

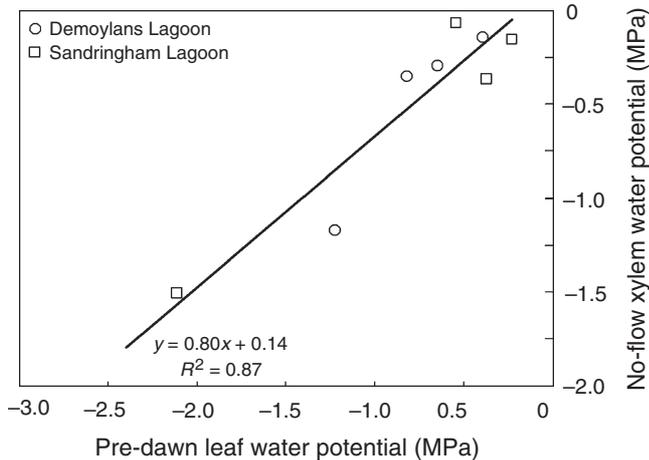


Fig. 2. Relationship between measured pre-dawn leaf water potential and the no-flow leaf water potential for trees at Demoylans and Sandringham Lagoon. No-flow water potential was estimated by extrapolating the relationship between flow and water potential to predict leaf water potential at zero flow.

Demoylans

Vegetation

Seven tree species were recorded in three 20×20 m plots. Basal area was $15.2 \pm 2.4 \text{ m}^2 \text{ ha}^{-1}$ and canopy cover was 64%. Four species; *Corymbia clarksoniana*, *Lophostemon suaveolens*, *Melaleuca viridiflora* and *Eucalyptus platyphylla* contributed over 95% of the stand basal area. The water level was 9.24 m below surface on 18 August 2003. Mean canopy condition at the site was 2.7, suggesting that canopy vegetation at this site was in a poor condition. There was little evidence of regeneration, suggesting a possible long-term decline in site condition.

Tree water use

Tree water use varied from less than 4 L day^{-1} in the small *M. viridiflora* trees to more than 76 L day^{-1} for the large *E. platyphylla*. $Q_{s \text{ max}}$ was highest in the *E. platyphylla* and *C. clarksoniana* trees (0.31 and $0.29 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$, respectively) and lowest in the subdominant *M. viridiflora* and *L. suaveolens* trees (0.18 and $0.13 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$, respectively). Examples of diurnal patterns of transpiration for each sample tree are shown in Fig. 3. Daily water use patterns appeared to reflect typical patterns of incoming radiation and changes in vapour pressure deficit (VPD) throughout the day. *L. suaveolens* trees exhibited a midday depression of transpiration. This response is typically related to stomatal control of transpiration in response to increased VPD and declining leaf water potential. *L. suaveolens* trees had the lowest pre-dawn leaf water potential, indicating a larger degree of water stress. There was a weak negative correlation

between pre-dawn leaf water potential and maximum transpiration rates (Fig. 4).

Comparison of soil and plant water potentials and ^{18}O

Figure 5 compares the soil and xylem water potentials, and the soil water, xylem water and groundwater isotopic compositions for each species at Demoylans. Two soil bores were augured at the Demoylans site: one down to 8.5-m depth and a second down to 4.5 m. Soil water potentials in Core 1 were between -2200 and -1200 kPa between the land surface and 7.0-m depth, and then increased to -280 kPa at 8.0–8.5-m depth. In Core 2, matric potentials were -2960 kPa at 0.5–1.0-m depth, -2100 kPa at 1.5–2.0-m depth and -1880 kPa at 4.0–4.5 m (Fig. 5). Soil matric potential shows good consistency between the two core sites, with significant variation apparent only in the shallow sample.

The ^{18}O composition of soil water decreases from -2.2‰ at 0.5–1.0-m depth, to a reasonably constant value of -4.0 to -4.2‰ between 3.0 and 8.5 m. No significant variation in isotopic composition was measured between the two core sites. A stable isotopic composition of -3.5‰ was measured on groundwater from Bore 12600025, located ~ 120 m from the Core 1. Oxygen-18 composition of twig water ranged between -2.7 and -4.2‰ , with a single outlier at -1.77‰ .

Corymbia clarksoniana had a minimum (midday) xylem water potential of -1.10 MPa . Soil water potentials were less than -1.10 MPa above 7-m depth; thus, soil water at depths less than 7 m would not be available to the plant during daily transpiration. The maximum leaf water potential of about -0.4 MPa and tree height of 5 m is consistent with water extraction from a source with matric potential greater (less negative) than -0.35 MPa . Thus, at this site, this species is solely relying on water below 7-m depth for transpiration, and is probably extracting water from close to the watertable. The isotopic composition of the xylem water was -4.05 to -4.19‰ , which is the lowest of the trees sampled. Although there is little variation in isotopic composition of soil water below 3 m, the xylem isotopic composition is consistent with water extraction from groundwater or from the capillary fringe.

Melaleuca viridiflora had a minimum xylem water potential of -1.75 MPa . Soil water potentials greater than this value occur between 0- and 0.5-m depth, and at depths below 3 m. The maximum xylem water potential was -0.68 MPa on this same tree, and was -0.58 and -0.63 MPa on other *Melaleuca* trees. Soil water potentials similar to or greater than this value occur below 7-m depth. Thus, the species is extracting some water from below 7-m depth, but may also be extracting water from between 3 and 7 m. The isotopic composition of xylem water was mostly between -3.4 and -4.0‰ , which is consistent with

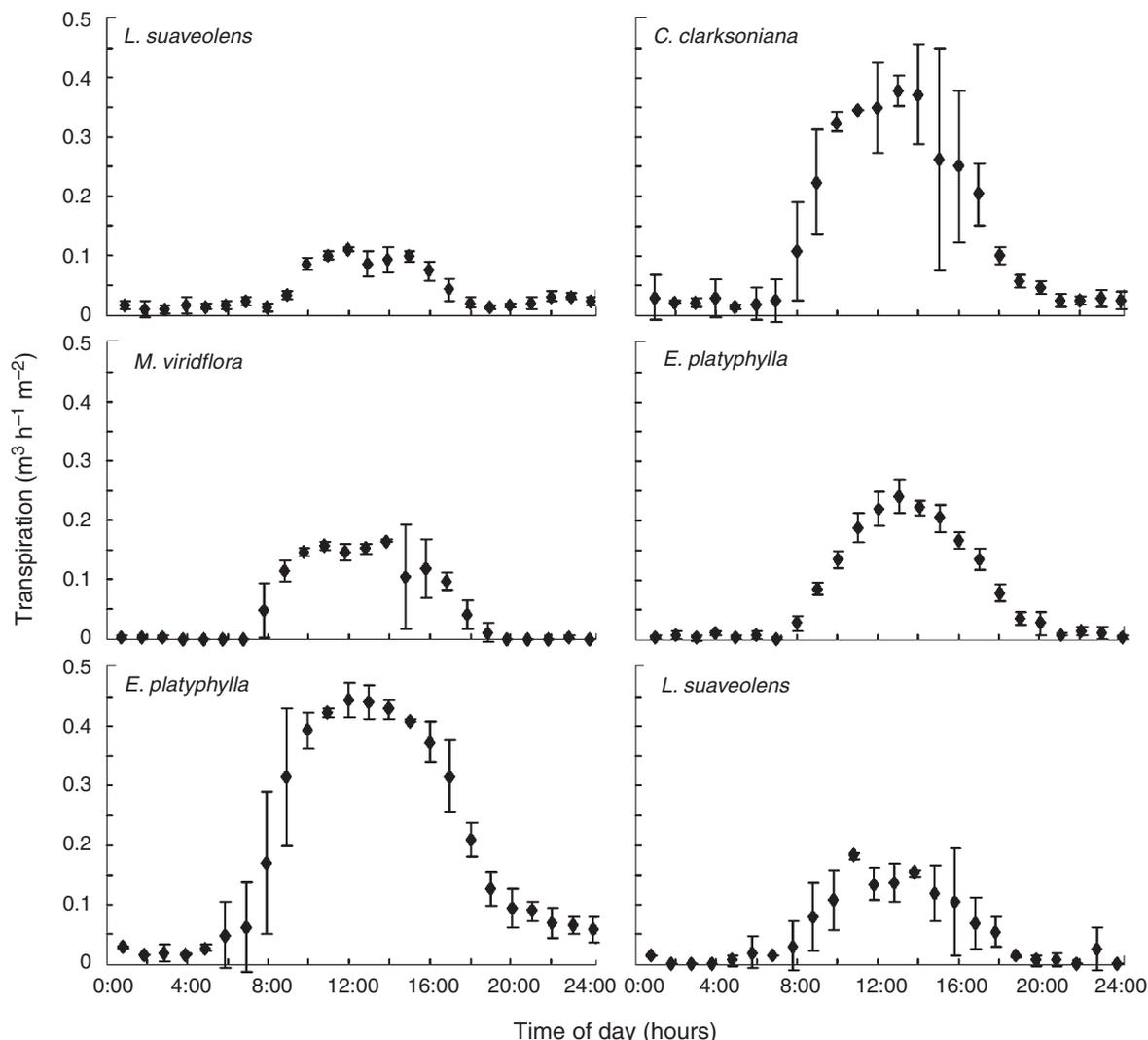


Fig. 3. Diurnal patterns of transpiration for selected trees at Demoylans.

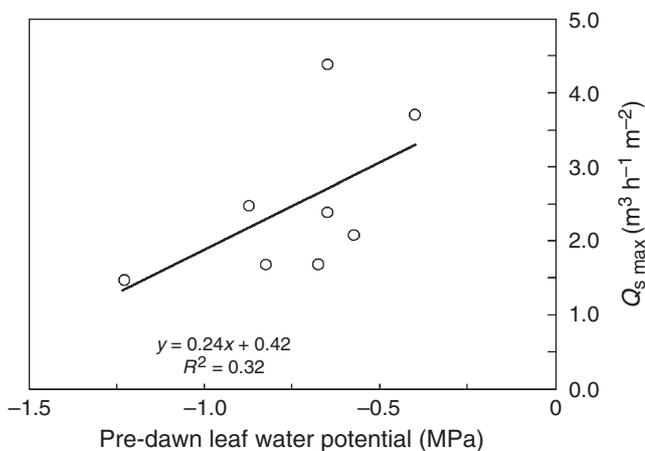


Fig. 4. Relationship between transpiration and pre-dawn leaf water potential for tree species at Demoylans.

water extraction from ~3-m depth. More likely, however, this isotopic composition reflects a mixture of water obtained from near the soil surface and from between 3 and 7 m. The single xylem ^{18}O value of -1.77‰ may indicate a source very close to the soil surface.

Lophostemon suaveolens and *E. platyphylla* had minimum xylem water potentials of -2.4 and -2.25 MPa, respectively. The maximum xylem water potentials were from -1.25 to -1.05 MPa (*L. suaveolens*) and from -0.65 to -0.88 MPa (*E. platyphylla*). Corresponding soil matric potentials indicate that the maximum depth accessed by *L. suaveolens* is probably 5–6 m. *E. platyphylla* may be extracting a small amount of water from as deep as 6–7 m. The isotopic composition of xylem water for these two species was more depleted than that for *C. clarksoniana* and *M. viridiflora*, reflecting an increased use of shallow soil water, which has an isotopic composition closer to zero. It is

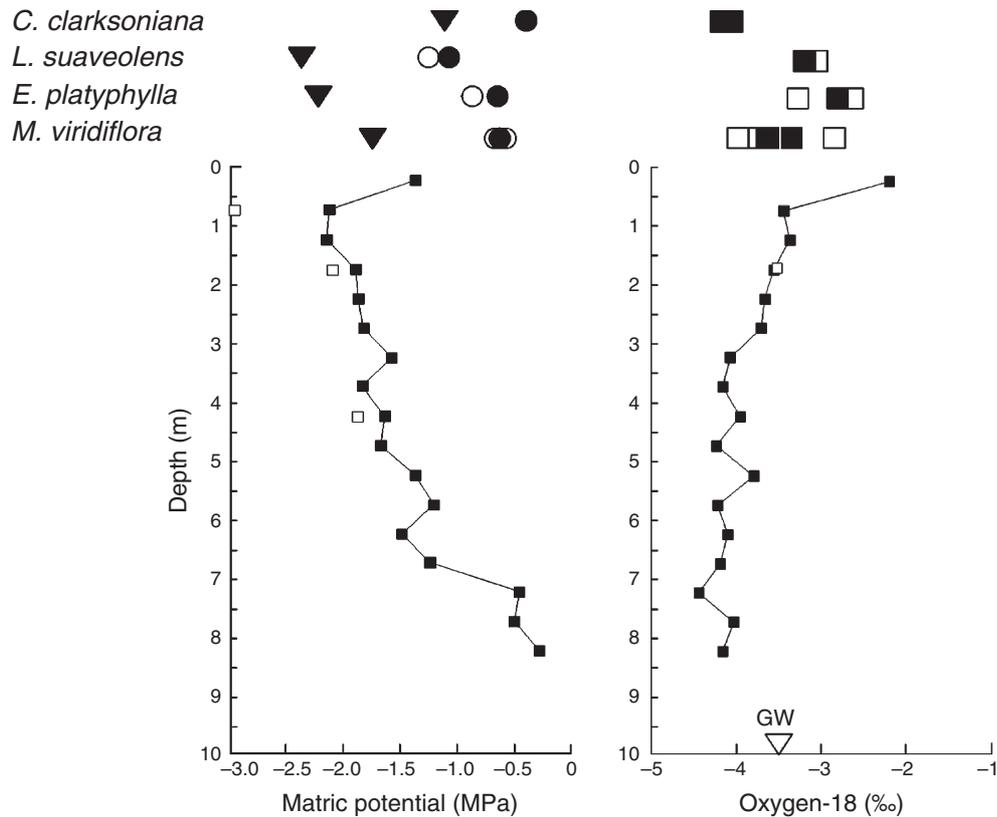


Fig. 5. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at Demoylans. For the four trees on which xylem water potentials were measured throughout the morning, minimum values are shown as solid triangles, and maximum values as solid circles. Solid squares denote xylem isotopic compositions on these same trees. Open circles and open squares denote maximum (pre-dawn) xylem water potentials and isotopic compositions, respectively, on the other sampled trees.

thus likely that these species were extracting most of their water from above 3-m depth.

Sandringham Lagoon

Vegetation

Five tree species were recorded in the three transects. Basal area at the site was $20.3 \pm 9.4 \text{ m}^2 \text{ ha}^{-1}$ and canopy cover was 64%. Three species, *Corymbia tessellaris*, *L. suaveolens* and *M. viridiflora*, contributed over 95% of the stand basal area at this site. Groundwater depth at the site is $\sim 4 \text{ m}$. Average canopy condition at the site was 3.0, suggesting that the vegetation at this site was in reasonable condition.

Tree water use

Daily water use varied from 6 L day^{-1} for a small *C. tessellaris* to more than 50 L day^{-1} for a large *C. tessellaris*. *L. suaveolens* had the lowest maximum transpiration rate ($0.22 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$). The highest rates were recorded in a *M. viridiflora* on the bank of the lagoon and a nearby *C. tessellaris* (0.37 and $0.57 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$, respectively). Examples of diurnal patterns of transpiration are shown in Fig. 6. Midday depression of transpiration was evident

in a small *C. tessellaris* and *L. suaveolens*. There was no correlation between pre-dawn leaf water potential and maximum transpiration rate at this site.

Comparison of soil and plant water potentials and ^{18}O

Figure 7 compares the soil and xylem water potentials, and the soil water, xylem water and groundwater isotopic compositions. A single auger hole was drilled to 4.0-m depth, $\sim 28 \text{ m}$ north of Sandringham Lagoon. Soil matric potentials were between -2800 kPa and -1200 kPa from the soil surface to 2.5-m depth. Below 2.5 m, matric potentials increased to close to saturation at 3.5–4.0 m. This core site was located only 1.05 m above the level of the lagoon, and yet the standing water level in the hole rose to only 3.53 m (thus the sample from 3.5–4.0 m is from below the watertable). A second soil core was drilled to 1.0-m depth, at a site $\sim 30 \text{ m}$ north of Core 1. The stable isotopic composition of soil water from Core 1 at Sandringham Lagoon is between -2.89 and -1.59‰ . A groundwater sample obtained from immediately beneath the watertable at 3.53-m depth had an isotopic composition of -2.47‰ , whereas the groundwater sample obtained from Bore 12600550 had an isotopic

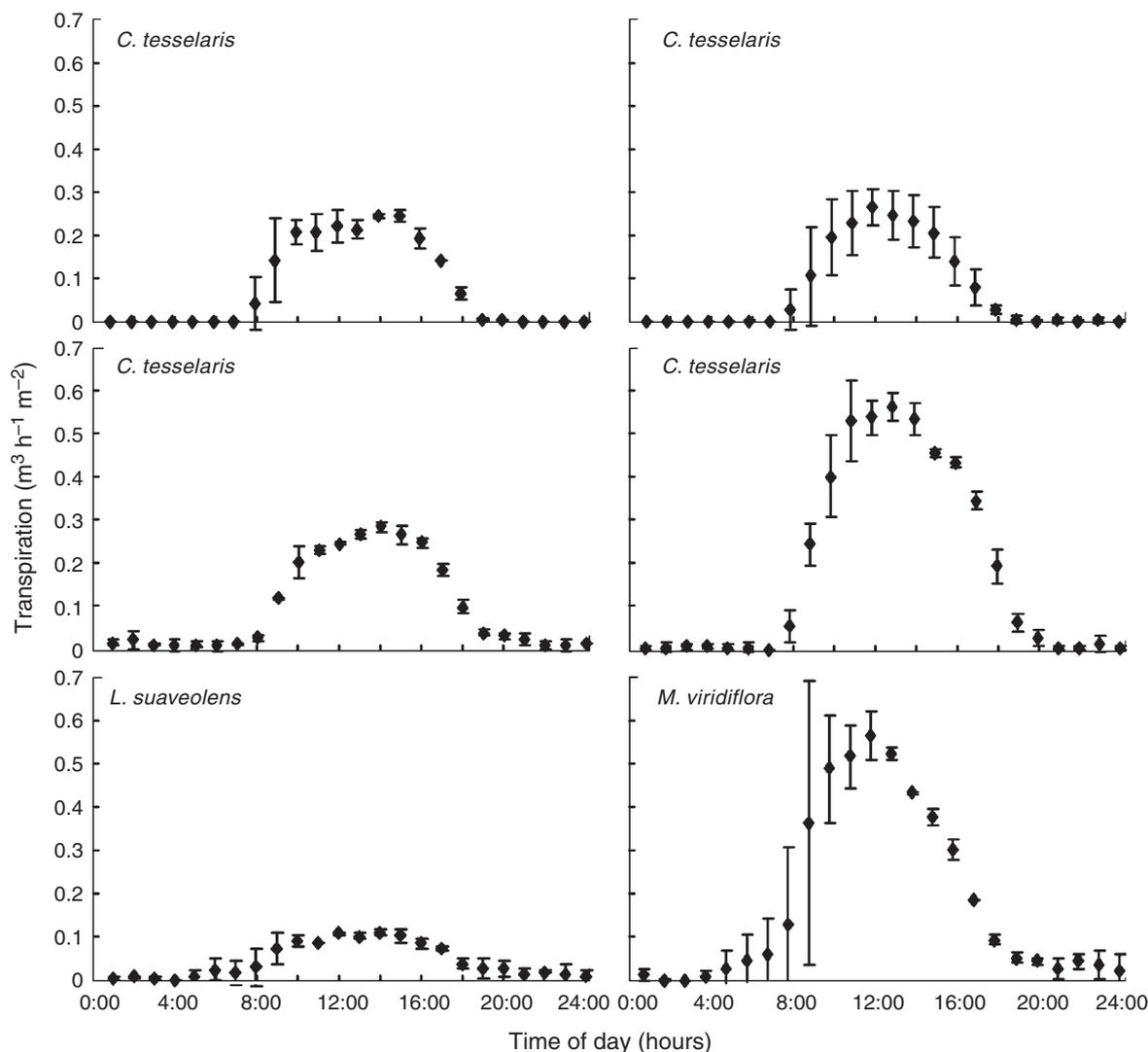


Fig. 6. Diurnal patterns of tree transpiration at Sandringham Lagoon.

composition of -2.92% . A surface water sample obtained from the lagoon had an isotopic composition of -2.27% .

Corymbia tessellaris had minimum xylem water potentials between -1.11 and -1.45 MPa. Soil water potentials are less than -1.11 MPa above 2.5-m depth, and so this soil water would not have been extracted during daily transpiration. The maximum xylem water potential varied between -0.23 and -0.38 MPa. Soil water potentials similar to or higher than this value occurred only below 3 m. Thus, at this site, *C. tessellaris* was reliant on water below 2.5-m depth for transpiration. The isotopic composition of the xylem water was from -2.81 to -2.34% . Although there is little variation in isotopic composition of soil water within the profile, the xylem isotopic composition is consistent with water extraction from groundwater or from the capillary fringe.

Melaleuca viridiflora on the edge of the lagoon had a minimum xylem water potential of -1.10 MPa. Soil water potentials higher than this value occur at depths below 2.5 m. The maximum xylem water potential was -0.55 MPa on this same tree, and -0.73 and -1.1 MPa on other *Melaleuca* trees, further from the lagoon. Soil water potentials similar to or greater than this value occur below 3-m depth. Thus, the *Melaleuca* species located further back from the lagoon are extracting some water from below 3-m depth. The isotopic composition of xylem water for the *M. viridiflora* on the lagoon edge was from -2.15 to -2.26% , whereas for the other *M. viridiflora* it was from -2.69 to -1.40% . These were similar to the isotopic composition of surface waters in Sandringham Lagoon and in shallow soil water, and so provided little discrimination. However, on the basis of its location and relatively large size, the

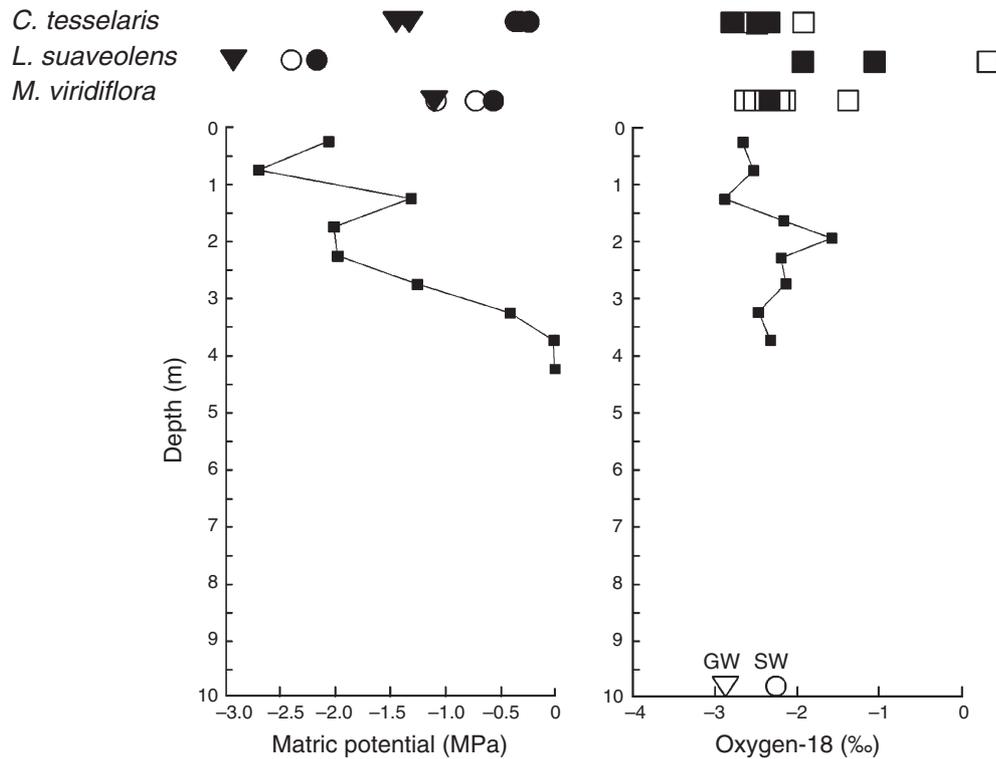


Fig. 7. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at Sandringham Lagoon. For the four trees on which xylem water potentials were measured throughout the morning, minimum values are shown as solid triangles, and maximum values as solid circles. Solid squares denote xylem isotopic compositions on these same trees. Open circles and open squares denote maximum (pre-dawn) xylem water potentials and isotopic compositions, respectively, on the other sampled trees.

M. viridiflora at the edge of the lagoon is believed to be accessing surface water.

Minimum xylem water potential in the *L. suaveolens* trees at this site was -2.95 MPa and the maximum was -2.17 MPa. Similar values of soil water potential occur between 1- and 3-m depth. Differences in water sources are also reflected in the isotopic composition of *Lophostemon* xylem water (-1.91 to $+0.35$ ‰), which is more enriched than the *Corymbia* and *Melaleuca* trees. While some xylem values are more enriched than measured values within the soil core, they presumably reflect shallow soil water values, which may show considerable spatial variability.

McGregor Creek

Vegetation

Twenty-one tree species were recorded in three transects. Basal area was $\sim 33.1 \pm 10.6$ m² ha⁻¹. *Lophostemon suaveolens* and *C. clarksoniana* together accounted for 65% of the site basal area. Average canopy cover was 74.9 ± 1.3 %. There were gradients in canopy cover along transects, ranging from 91.9% immediately adjacent to the creek to 55.9% at the top of the terraces. Average canopy condition at this site was 3.8, indicating that vegetation

at this site could be considered to be in relatively good condition. Several species, including *Aphananthe philippinensis*, *Melaleuca leucadendra*, *Cryptocarya hypospodia* and *Casuarina cunninghamiana*, scored 5, the highest condition rating on this scale.

The water level in nearby Bore 12500065 mostly varies between ~ 7.5 and 10 m, and was 9.78 m on 27 August 2003. Watertable depths were also measured in two auger holes established at the site. In Core 1, located ~ 75 m from the riverbank, the watertable was at 6.99-m depth. In Core 2, located on a river terrace ~ 5 m from the riverbank, the watertable was at 4.14-m depth.

Tree water use

Tree water use was recorded in a total of 10 trees from seven species at McGregor Creek and rates varied from less than 3 L day⁻¹ for a sapling *E. platyphylla* to more than 130 L day⁻¹ in a *C. clarksoniana* (Table 2). Examples of diurnal patterns of transpiration are shown in Fig. 8. Hourly transpiration rates were highest (0.6 m³ h⁻¹ m⁻²) in the *Corymbia* trees and were lowest (0.16 m³ h⁻¹ m⁻²) in a *M. leucadendra* tree. There was a negative correlation between pre-dawn leaf water potential and maximum daily transpiration rate (Fig. 9).

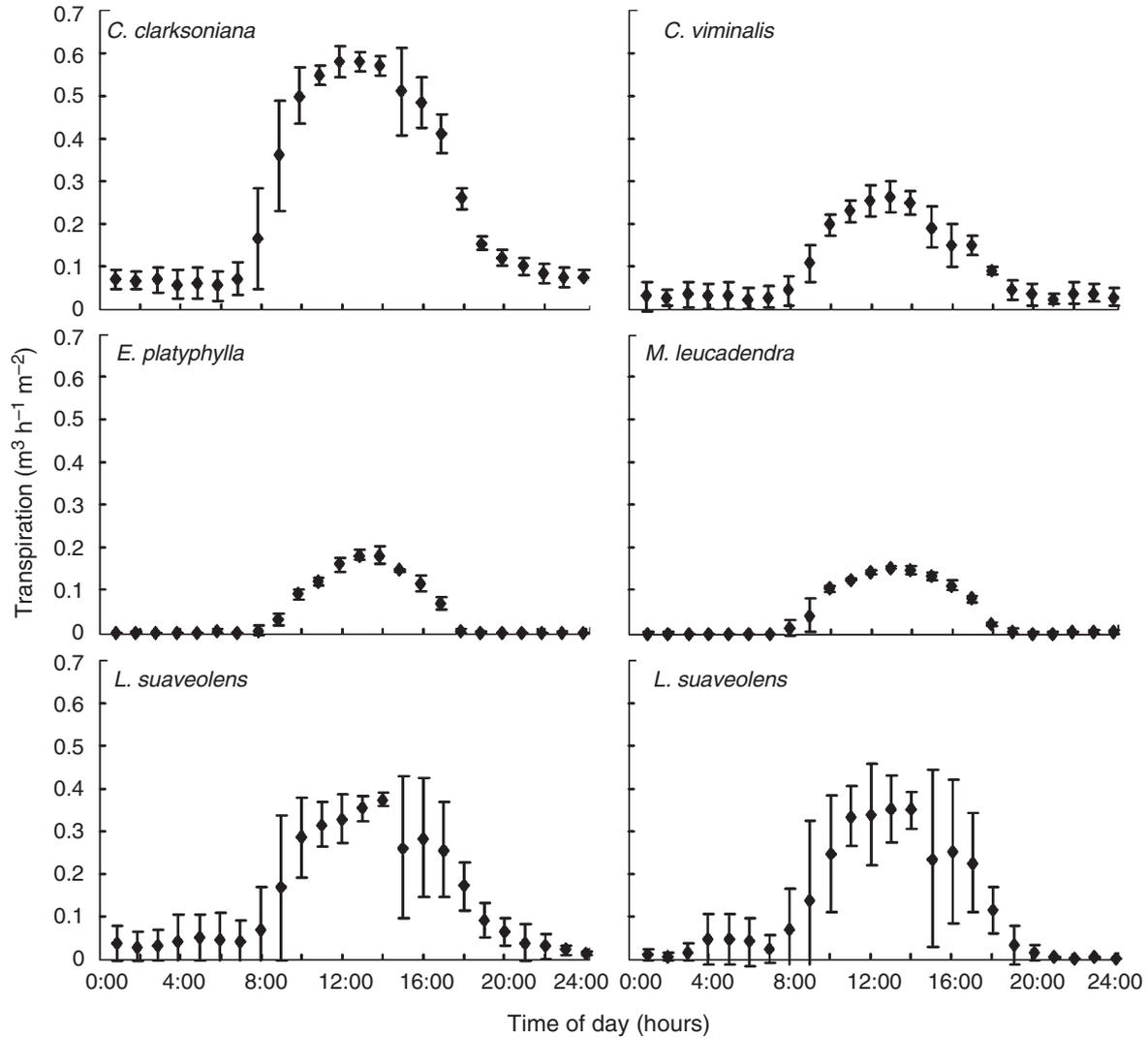


Fig. 8. Diurnal patterns of transpiration for selected trees at McGregor Creek.

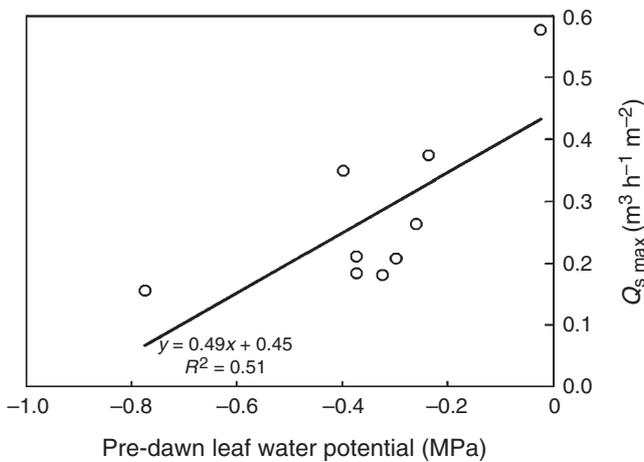


Fig. 9. Relationship between tree water use and pre-dawn leaf water potential for trees at McGregor Creek.

Comparison of soil and plant water potentials and ¹⁸O

Two cores were augured at McGregor Creek. Core 1 was located ~75 m from the riverbank, at an elevation of 7.2 m above river level. Soil water potentials were between -1700 and -700 kPa between the land surface and 4.5-m depth, increasing to approximately -60 kPa at 5.5–6.5 m (Fig. 10). The standing-water level was measured at 6.99 m. Core 2 was augured on a river terrace ~5 m from the riverbank and 4.1 m above the river level. Between the soil surface and 3.0-m depth, matric potentials were between 12 and 25 kPa. Below 3.0-m depth, water contents and matric potentials increased. After drilling, the standing-water level rose to 4.14-m depth. Oxygen-18 ratios in soil water showed significant variations within the soil profiles (Fig. 11). At Core 1, values decreased from -3.5 to -4.1‰ above 2.0-m depth, to -4.1 to -4.9‰ between 5.0- and 8.0-m depth. In Core 2, ¹⁸O values decreased from -6.2‰ at 0.5–1.0-m

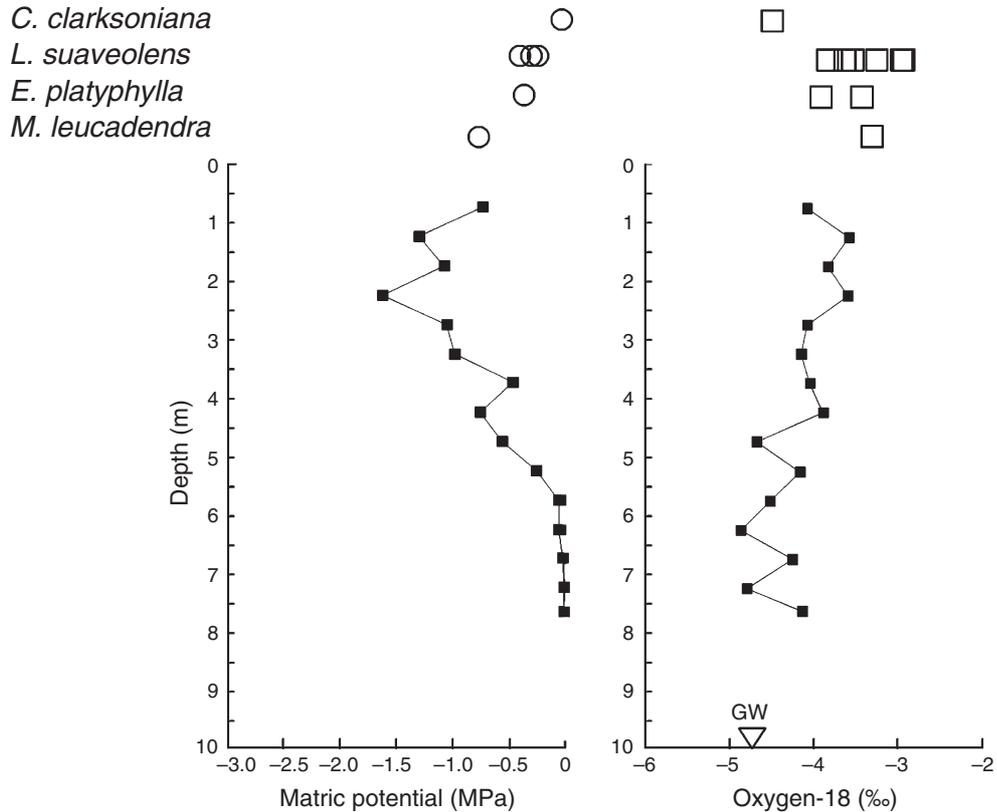


Fig. 10. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at upper terrace site of McGregor Creek.

depth, to -8.4‰ at 1.5–2.0-m depth. Below 2.0 m, values increased up to -5.0‰ at 3.5–4.0 m, immediately above the watertable at 4.14 m. Groundwater composition across the site was relatively uniform. Groundwater collected from standing water in Core 1 was -4.77‰ , whereas at Core 2 it was -4.91‰ . A groundwater sample collected from Bore 12500065, located ~ 80 m from Core 2 had an ^{18}O value of -4.97‰ . In contrast, creek water was more enriched, at -3.37‰ .

Pre-dawn leaf water potentials measured at McGregor Creek were relatively high, ranging between -0.78 and -0.03 MPa. The *Lophostemon* trees, located close to Core 1, had leaf water potentials between -0.40 and -0.24 MPa. A *M. leucadendra*, ~ 75 m from the stream, had the lowest leaf water potential of -0.78 MPa. The highest leaf water potential (-0.03 MPa) was measured at the site was for the *C. clarksoniana*, which was located between Cores 1 and 2, at an elevation of ~ 8.0 m above the river level.

Trees on the upper terrace of McGregor Creek exhibited a range of water sources (Fig. 10). *C. clarksoniana* had the highest leaf water potential and lowest isotopic composition. Minimum xylem water potential was -0.025 MPa, which indicated water uptake from saturated or near saturated depths in the soil profile (>6 m). The isotopic composition of

xylem water (-4.5‰) was similar to the isotopic composition of groundwater or soil water below 4.5 m. For *L. suaveolens* and *E. platyphylla* maximum water potential ranged between -0.24 and -0.4 MPa, suggesting access to water below 5-m depth. However, the isotopic composition of xylem water for *E. platyphylla* was between -3.44 and -3.93‰ and for the *L. suaveolens* between -3.85 and -2.94‰ . This was more enriched than water from depths below 5 m, and reflected the isotopic composition of soil water above 3-m depth. Matric potentials were lowest between 1.0- and 3.0-m depth, which suggested a zone of high water extraction between these depths. It is likely that *L. suaveolens* and *E. platyphylla* were extracting soil water from this zone although pre-dawn leaf water potential reflected soil water sources with the higher potentials, suggesting that some roots may extend down to almost 5-m depth. A small *M. leucadendra* away from the creek had the lowest pre-dawn xylem water potential, suggesting that its roots may be shallower than those of *L. suaveolens* and *E. platyphylla*. The isotopic composition of its xylem water was also consistent with water extraction from above 5 m. The isotopic composition of *Casuarina cunninghamiana* and *Cryptocarya hypospodia*, on the lower terrace, would indicate use of surface water from McGregor Creek. The

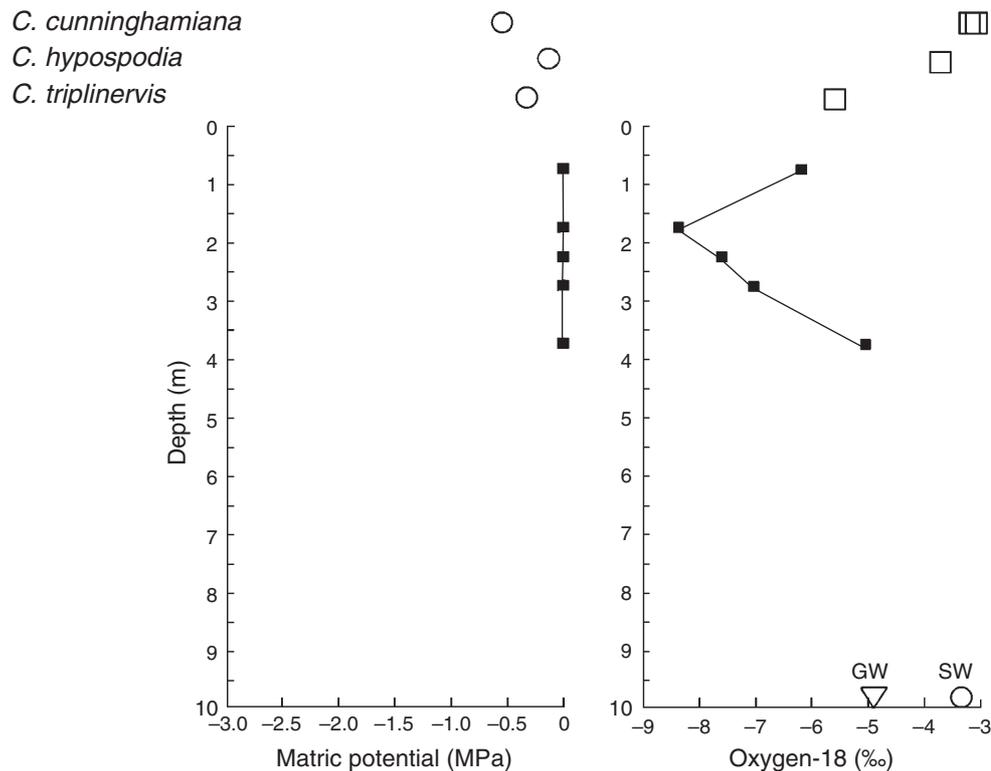


Fig. 11. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at the lower terrace site of McGregor Creek.

Cryptocarya triplinervis has an isotopic composition most consistent with groundwater use (Fig. 11).

Orchidways

Vegetation

Fourteen tree species were recorded along three transects. Basal area at this site was extremely variable. Average basal area at the site was $144.4 \pm 81.1 \text{ m}^2 \text{ ha}^{-1}$. *M. leucadendra* was the largest contributor to stand basal area, contributing more than 86% of the total basal area in the three surveyed transects. Canopy cover was 91.9%. Average canopy condition for trees at Orchidways was 4.0. Canopy condition of trees at this site was good.

Between 18 September and 3 November 2003, the water level in Bore 12600549, located at the top of the bank $\sim 30 \text{ m}$ south of Sandy Creek, ranged between 15.66- and 15.71-m depth. An auger hole (Core 1) drilled to 6-m depth, and located $\sim 3 \text{ m}$ south of the creek had a standing water level of 4.58 m on 27 August 2003. A potentiometer indicated that the groundwater level in the hole was 10.2 cm higher than the creek water level at that time. The watertable depth thus varies depending on location along the transect.

Tree water use

Tree water use was measured in 10 trees of six species (Table 2). Tree water use varied from less than

1 L day^{-1} for a small shaded *Callistemon viminalis*, to more than 200 L day^{-1} for a large *M. leucadendra* tree on the riverbank. Diurnal patterns of transpiration are shown in Fig. 12. The highest rates of transpiration were observed in the *E. platyphylla* and *A. philippinensis* ($>0.6 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$). Although *A. philippinensis* had a high maximum transpiration rate, it also had a low pre-dawn leaf water potential (-1.55 MPa). The diurnal curve for *A. philippinensis* reflected a water-use strategy different from other trees in the stand. Transpiration rates increased quickly in the morning to a maximum but then declined sharply almost immediately. In contrast, other trees in the stand with low pre-dawn leaf water potential either had lower maximum rates of transpiration or exhibited a midday depression of transpiration. The lowest rates of transpiration were observed in *Macaranga tanarius* ($<0.1 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$). Maximum transpiration rates were relatively uniform for the *Melaleuca leucadendra* trees ($\sim 0.2 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$).

Comparison of soil and plant water potentials and ^{18}O

Two cores were obtained from the Orchidways site: Core 1 (Fig. 13) on the lower terrace and Core 2 (Fig. 14) on the upper terrace. Figure 14 depicts water potentials for Core 2, where the watertable was estimated to be at $\sim 11.8\text{-m}$ depth. Soil water potentials were between -1500 and -1000 kPa at

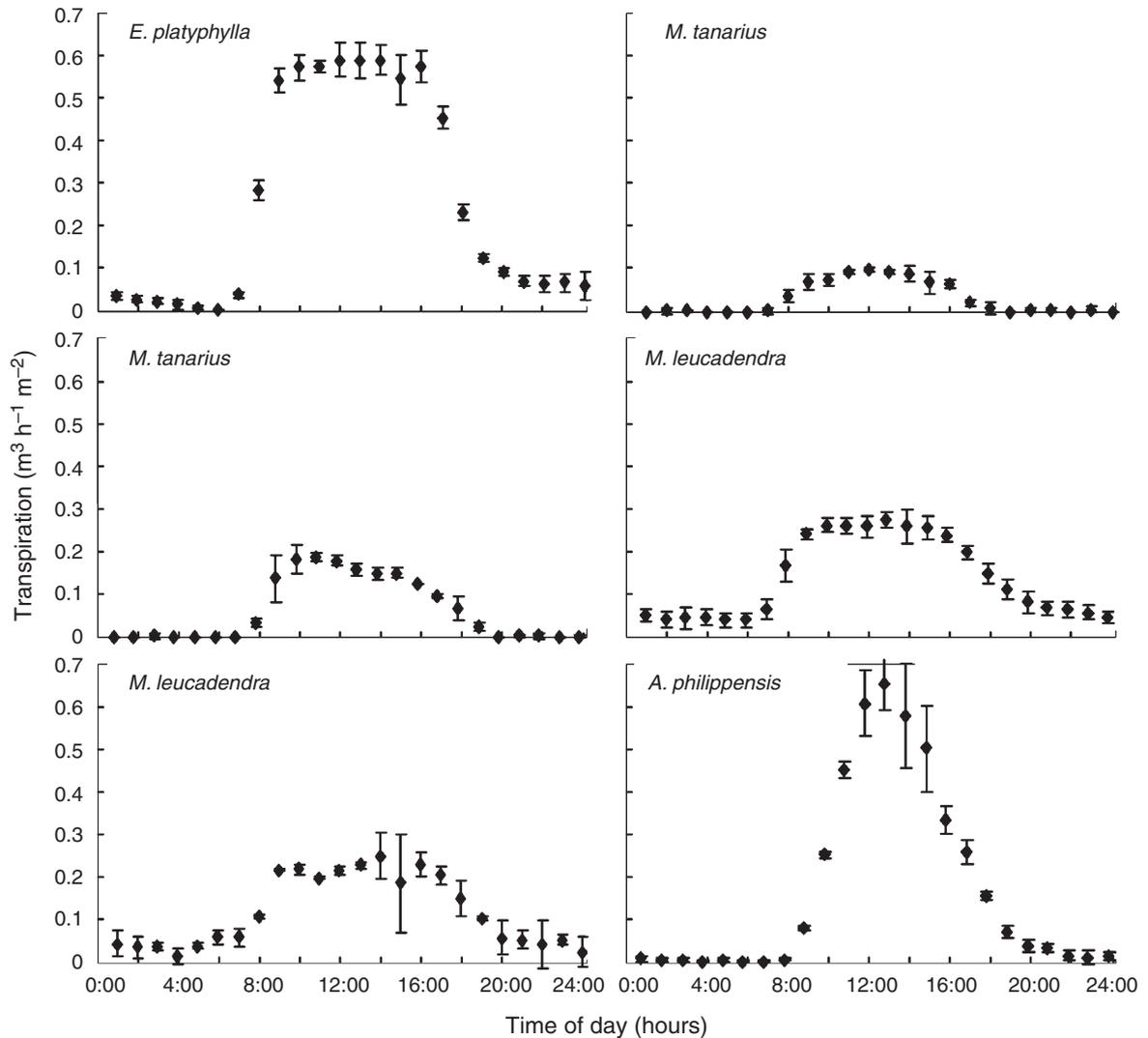


Fig. 12. Diurnal patterns of transpiration for selected trees at Orchidways.

0.5–4.0-m depth, increasing to -830 to -700 kPa between 4.0- and 6.5-m depth. Oxygen-18 values of soil water were between -3.2 and -5.0 ‰, except for a single sample with an ^{18}O value of -1.97 ‰ at 4.5–5.0 m, possibly the result of analytical error. At Core 1 soil water potentials were between about -1000 and -500 kPa between the land surface and 2.5-m depth, increasing to values higher than -50 kPa below 4.0 m (Fig. 14). The watertable was at 4.58 m. The ^{18}O composition of soil water was highly variable, ranging between approximately -6.5 ‰ between 0.5- and 1.5-m depth, and approximately -3.5 ‰ at 2.5- to 4.0-m depth. A groundwater sample obtained from immediately below the watertable at this site had ^{18}O composition of -4.75 ‰. The ^{18}O composition of groundwater from Bore 12600549 was -4.29 ‰. The surface water had an ^{18}O composition of -3.60 ‰.

Callistemon viminalis, *Psidium guajava* and *Macaranga tanarius* and *Melaleuca leucadendra* were all located on the lower river terrace, either close to Core 1 or at similar elevations. *M. tanarius* had a pre-dawn leaf water potential of -0.23 MPa. Soil matric potentials representative of these values occur only below 3.5-m depth, indicating either deep soil water or groundwater use. Its xylem isotopic composition (-3.85 ‰) is consistent with water extraction from between 2.5- and 4.5-m depth (Fig. 13). It is thus likely that this species is sourcing most of its water from groundwater. *C. viminalis* had pre-dawn leaf water potentials of -0.55 MPa. This value is relatively low, considering its positions in the landscape (close to the river). Maximum transpiration rates were also low ($0.031 \text{ m}^3 \text{ h}^{-1} \text{ m}^{-2}$). Although xylem isotopic composition was consistent with water extraction from below 2.5 m, leaf water potential suggested that it was not extracting

C. viminalis
P. guajava
M. tanarius
M. leucadendra

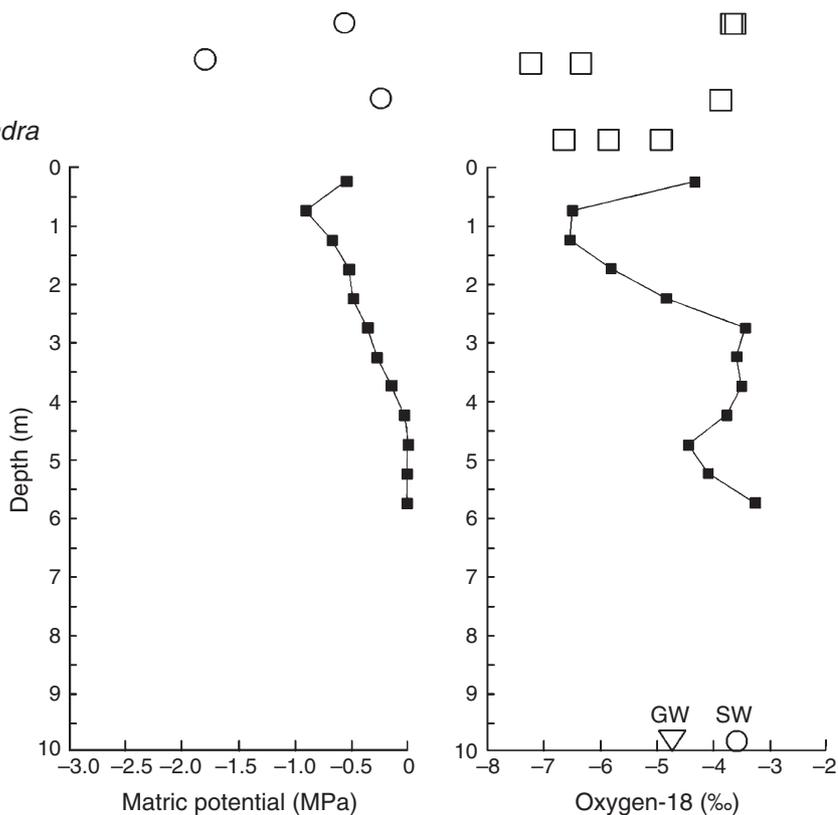


Fig. 13. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at lower site at Orchidways.

E. platyphylla
M. tanarius

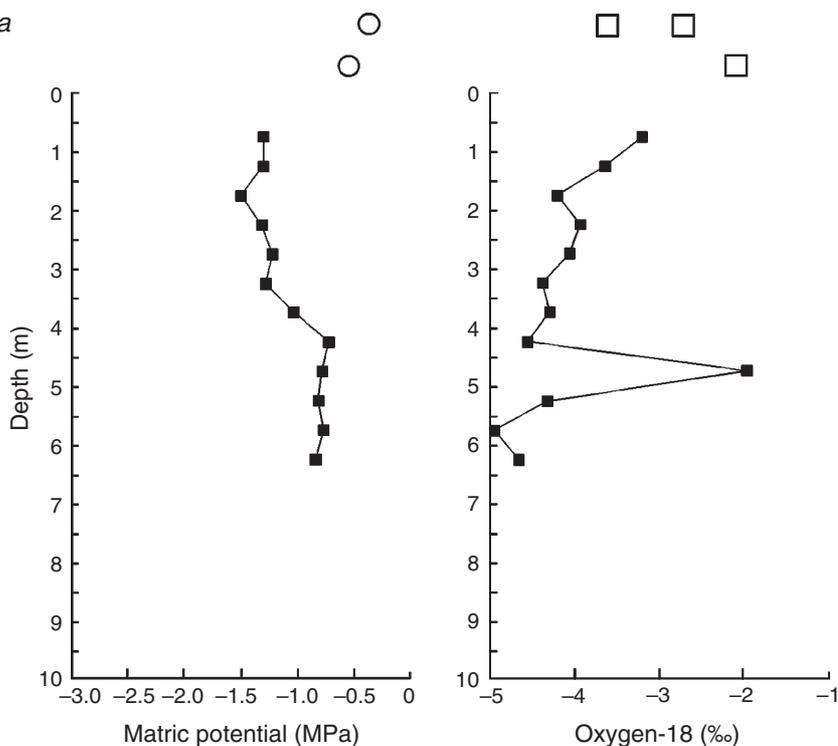


Fig. 14. Comparison of surface water, groundwater, soil water and xylem water potentials and isotopic compositions at upper site at Orchidways.

groundwater. *P. guajava* and *A. philippinensis* had pre-dawn leaf water potentials of -1.80 and -1.55 Mpa, respectively, suggesting soil water use. Their xylem isotopic compositions are consistent with exclusive use of shallow (1–2 m) soil water. Pre-dawn leaf water potentials were not measured on *M. leucadendra* in this topographic position because of difficulties in accessing the canopies of these large trees. The xylem isotopic composition was variable (-4.90 to -6.68‰). It was not possible to categorically determine the source of its water use. A *M. leucadendra* located on a sandy drift within the river channel (although 0.7 m above the river level at the time of survey) had a pre-dawn leaf water potential of -0.05 MPa, which is consistent with a water source close to saturation.

Two trees were located close to Core 2 obtained from higher up the bank. *E. platyphylla* and *M. tanarius* had pre-dawn leaf water potentials of -0.40 and -0.55 Mpa, respectively. Soil matric potentials were lower than -0.7 MPa down to at least 6.5-m depth (the limit of drilling), indicating that these species are accessing a water source deeper in the soil profile. However, the isotopic composition of xylem water (-2.74 to -3.61‰ and -2.11‰ for *E. platyphylla* and *M. tanarius*, respectively) was significantly different from that of groundwater (-4.29‰). Thus, it was considered unlikely that these trees were accessing groundwater.

Water sources for transpiration

Water sources of the dominant tree species are summarised in Fig. 15. Data presented here indicated that *C. clarksoniana* were using groundwater at Demoylans, where the groundwater was at 10-m depth, and at McGregor Creek where the watertable was at 7 m. Clearly, this species is able to access groundwater down to at least 10-m depth. *C. tessellaris* trees at Sandringham were using groundwater, where the watertable was at ~ 4 -m depth. However, this was the only site at which this species was sampled. Thus, we

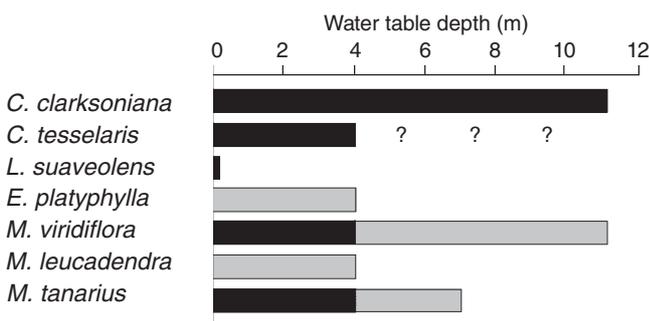


Fig. 15. Ranges of watertable depths that can be accessed by major tree species in the Pioneer Valley in August 2003. Black bars indicate strong evidence of groundwater use, whereas light-grey bars indicate weaker evidence. Question marks for *Corumbia tessellaris* indicate that this species was not sampled where watertable depths exceeded 4 m.

were unable to define a range of potential extraction depths for *C. tessellaris*.

Lophostemon suaveolens did not appear to be using groundwater at Sandringham (watertable at 4-m depth), McGregor Creek (watertable at 7-m depth) or Demoylans (watertable at 10-m depth). *E. platyphylla* was not using groundwater at McGregor Creek (watertable at 7-m depth) or Demoylans Lagoon (watertable at 10-m depth), but was not sampled at sites with shallower watertables. Anecdotal evidence suggests that this species is shallow-rooted, and thus is unlikely to be an obligate groundwater user.

Melaleuca viridiflora trees were using groundwater at Sandringham Lagoon (watertable at 4-m depth) and possibly at Demoylans (watertable at 10-m depth), suggesting that this species will use groundwater where it is available. *M. leucadendra* were possibly using groundwater at Orchidways (watertable at 4-m depth), but not at McGregor Creek (watertable at 7-m depth, although $n=1$). This species is typically restricted to rivers or permanent water sources, suggesting that it is highly reliant on permanent water. *Macaranga tanarius* on the lower terrace at Orchidways was using groundwater (watertable at 4-m depth). However, further up the bank (watertable at 12-m depth), it appeared to be largely reliant on soil water. At McGregor Creek, *Casuarina cunninghamiana* was using river water. *Cryptocarya hypospodia* was also using river water at McGregor Creek. *Callistemon viminalis* was not using groundwater at Orchidways, but this species tends to be restricted to creeks and permanent water sources.

Discussion

There were no general relationships between depth to groundwater and transpiration or depth to groundwater and pre-dawn leaf water potential. There was considerable spatial variability in the potential sources of water between remnant communities and within the remnant communities of the Pioneer Valley.

At all four sites, some tree species were using groundwater for transpiration. At Demoylans, only *C. clarksoniana* appeared to be a major groundwater user, even though this species contributed up to one-third of the standing basal area of this woodland community. At Sandringham Lagoon both *C. tessellaris* and *M. viridiflora* appeared to be using groundwater. These species together represent 72% and the community basal area of $20\text{ m}^2\text{ ha}^{-1}$, indicating that this community is strongly groundwater dependent. Both Sandringham and Demoylans are subject to annual inundation periods, thus groundwater may be particularly important during drought. Generally, soil water would be recharged during the wet season. Cook *et al.* (1998) demonstrated that there was sufficient water stored in the soil profile to maintain transpiration during the dry season in the *E. miniata*–*E. tetradonta* open-forests in the Northern Territory. At Demoylans the watertable was ~ 9 m below the

surface, although this varies depending on the preceding wet seasons. Rainfall for the previous two wet seasons was well below average (820 and 915 mm in 2001 and 2002, respectively) and groundwater use by *C. clarksoniana* at this site may reflect the failure of the previous wet seasons to recharge the soil water store.

At McGregor Creek, *C. clarksoniana* were using groundwater, but only represented 17% of the community basal area. *L. suaveolens* and *E. platyphylla* were possibly using groundwater. These species together comprised a further 53% of the community basal area. Although at the time of sampling, the hydraulic gradient was away from the river, i.e. water was probably flowing out of the creek into the groundwater, owing to upstream releases of water into McGregor Creek, at other times of year it is likely that groundwater flows into the creek and is important for maintaining the complex riparian forests along this creek. *Casuarina cunninghamiana* and *Cryptocarya hypospodia* were sourcing river water for transpiration at the time of sampling. At Orchidways on Sandy Creek, *M. tanarius* was clearly groundwater dependent, but represented only a small component of the community ($0.55 \text{ m}^2 \text{ ha}^{-1}$ of the total basal area of $144 \text{ m}^2 \text{ ha}^{-1}$). The results for *M. leucadendra*, which is a large component of the community basal area (basal area $124 \text{ m}^2 \text{ ha}^{-1}$), were inconclusive; however, one tree was clearly using river water, and groundwater discharge is a significant component of river baseflow at this site.

Riparian species tend to be opportunistic in the sources of water they are able to use. Lamontagne *et al.* (2005) demonstrated that groundwater use by riparian species along the Daly River in the Northern Territory was principally a function of position in the landscape. Two species, *Casuarina cunninghamiana* and *Acacia auriculiformis* used groundwater when it was shallow but used soil water at higher positions in the landscape. Similarly, Zencich *et al.* (2002) demonstrated that sources of water used by Banksia species on the Gngangara mound varied as a function of species, season and position in the landscape. In this study it has been difficult to assess the relationship between depth to groundwater and sources of water used by plants; however, riparian communities of McGregor Creek exhibited structural zonation with increased distance and height above the river that may reflect varying access to reliable groundwater. Canopy cover was higher at low positions and trees were generally accessing groundwater or river water; however, canopy cover was lower at higher positions in the landscape and species were accessing soil water and groundwater.

Conclusions

Predicting the nature of groundwater dependence and estimating annual rates of groundwater use in terrestrial vegetation is difficult without an understanding of the

temporal and spatial nature of tree water use and the temporal contribution of groundwater to transpiration. This study has examined some aspects of the spatial variability associated with groundwater use and has highlighted the potential importance of groundwater in the hydrological cycle of remnant vegetation in the Pioneer Valley. However, groundwater water use is likely to be a function of several factors, including depth to watertable (Zencich *et al.* 2002), maximum rooting depth for each species, the rooting distribution (Groom 2004) and soil water reserves (Cook *et al.* 1998). A complete assessment of groundwater dependence of these communities requires a better understanding of the spatial and temporal patterns of water use and the sources of water used.

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References

- Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC, Bustamante M (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* **24**, 891–899.
- Clear R (2000) Pioneer catchment rehabilitation project. A Pioneer Integrated Catchment Management Association Initiative, University of Queensland, Gatton, Qld.
- COAG [Council of Australian Government] (1996) Allocation and use of groundwater: a national framework for improved groundwater management in Australia. Occasional Paper Number 2. Council of Australian Government, Canberra, Australia.
- Cook PG, Hatton TJ, Pidsley D, Herczeg AL, Held A, O'Grady A, Eamus D (1998) Water balance of a tropical woodland ecosystem, northern Australia: a combination of micro-meteorological, soil physical and groundwater chemical approaches. *Journal of Hydrology* **210**, 161–177. doi: 10.1016/S0022-1694(98)00181-4
- Cramer VA, Hobbs RJ (2002) Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: impacts and possible management responses. *Austral Ecology* **27**, 546–564. doi: 10.1046/j.1442-9993.2002.01215.x
- Dawson TE, Ehleringer JR (1991) Streamside trees that do not use streamwater. *Nature* **350**, 335–337. doi: 10.1038/350335a0
- Donovan LA, Linton MJ, Richards JH (2001) Pre-dawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. *Oecologia* **129**, 328–335.
- Edwards WRN, Warwick NWN (1984) Transpiration from a kiwi fruit vine as estimated by the heat pulse technique and the penman monteith equation. *New Zealand Journal of Agricultural Research* **27**, 537–543.
- Greacen EL, Walker GR, Cook PG (1989) Procedure for filter paper method of measuring soil water suction. CSIRO Division of Soils, Divisional Report 108, Adelaide.
- Groom PK (2004) Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Functional Plant Biology* **31**, 423–428. doi: 10.1071/FP03200

- Hatton TJ, Evans R (1998) Dependence of ecosystems on groundwater and its significance to Australia. Occasional Paper 12/98, Land and Water Research and Development Corporation, CSIRO, Australia. LWRRDC, Canberra.
- Hatton TJ, Catchpole EA, Vertessy RA (1990) Integration of sap flow velocity to estimate plant water use. *Tree Physiology* **6**, 201–209.
- Hunt MA, Beadle CL (1998) Whole tree transpiration and water use partitioning between *Eucalyptus nitens* and *Acacia dealbata* weeds in short rotation plantation in northeastern Tasmania. *Tree Physiology* **18**, 557–564.
- Hutley LB, O'Grady AP, Eamus D (2000) Daily and seasonal patterns of evapotranspiration from eucalypt open forest savanna of tropical northern Australia. *Functional Ecology* **14**, 183–194. doi: 10.1046/j.1365-2435.2000.00416.x
- Köstner BM, Granier A, Cermák J (1998) Sapflow measurements in forest stands: methods and uncertainties. *Annales Des Sciences Forestieres* **55**, 13–27.
- Lamontagne S, Cook PG, O'Grady AP, Eamus D (2005) Determination of groundwater use in a tropical savanna riparian zone (Daly River, Australia). *Journal of Hydrology* **310**, 280–293.
- Lemon PE (1957) A new instrument for measuring forest overstorey density. *Journal of Forestry* **55**, 667–668.
- Moore SA, Renton S (2002) Remnant vegetation, landholders' values and information needs: an exploratory study in the West Australian wheatbelt. *Ecological Management & Restoration* **3**, 179–187. doi: 10.1046/j.1442-8903.2002.00111.x
- Myers BJ, Theiveyanathan S, O'Brien ND, Bond WJ (1996) Growth and water use of *Eucalyptus grandis* and *Pinus radiata* plantations irrigated with effluent. *Tree Physiology* **16**, 211–219.
- O'Grady AP (2000) Patterns of tree water use and stand water use in the eucalypt open-forests of northern Australia. PhD Thesis, Northern Territory University, Darwin.
- O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases in the dry season: patterns of tree water use in the eucalypt open forests of Northern Australia. *Tree Physiology* **19**, 591–597.
- Revesz K, Woods PH (1990) A method to extract soil water for stable isotope analysis. *Journal of Hydrology* **115**, 397–406. doi: 10.1016/0022-1694(90)90217-L
- Ritchie GA, Hinckley TM (1975) The pressure chamber as an instrument for ecological research. *Advances in Ecological Research* **9**, 165–254.
- Schulze E, Hall AE (1982) Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In 'Physiological plant ecology II: water relations and carbon assimilation'. (Eds OL Lange, PS Noble, CB Osmond, H Zeigler) pp. 181–230. (Springer-Verlag: Berlin)
- Smith DM, Allen AJ (1996) Measurement of sapflow in stems. *The Journal of Experimental Biology* **47**, 1833–1844.
- Sternberg LSL, Swart PK (1987) Utilization of freshwater and ocean water by coastal plants of southern Florida. *Ecology* **68**, 1898–1905.
- Swanson RH, Whitfield DWA (1981) A numerical analysis of heat pulse velocity theory and practice. *Journal of Experimental Botany* **32**, 221–239.
- Thorburn PJ, Hatton TJ, Walker GR (1993) Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. *Journal of Hydrology* **150**, 563–587. doi: 10.1016/0022-1694(93)90126-T
- Vertessy RA, Hatton TJ, Reece P, O'Sullivan SK, Benyon RG (1997) Estimating stand water use of large mountain ash trees and validation of the sapflow measurement technique. *Tree Physiology* **17**, 747–756.
- Werren GI (2001) Pioneer Valley Water Resources Plan: current environmental conditions and impacts of existing water resource development. Appendix F: riparian vegetation. Queensland Department of Natural Resources and Mines, Brisbane.
- Wullschlegel SD, Meinzer FC, Vertessy RA (1998) A review of whole plant water use studies in trees. *Tree Physiology* **18**, 499–512.
- Zencich SJ, Froend RH, Turner JV, Gailitis V (2002) Influence of groundwater depth on the seasonal sources of water accessed by Banksia tree species on a shallow, sand coastal aquifer. *Oecologia* **131**, 8–19. doi: 10.1007/s00442-001-0855-7

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