1 **Transpiration of *Eucalyptus* woodlands across a natural gradient**

2 **of depth-to-groundwater**

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18 **Running head:**   Impact of groundwater depth on transpiration

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Abstract

Water resources and their management present social, economic and environmental challenges, with demand for human consumptive, industrial and environmental uses increasing globally. However environmental water requirements, that is, the allocation of water to the maintenance of ecosystem health, are often neglected or poorly quantified. Further, transpiration by trees is commonly a major determinant of the hydrological balance of woodlands but recognition of the role of groundwater in hydrological balances of woodlands remains inadequate, particularly in mesic climates.

In this study we measured rates of tree water use and sapwood ^{13}C discrimination in a mesic, temperate Eucalypt woodland along a naturally-occurring gradient of depth-to-groundwater (DGW), to examine daily, seasonal and annual patterns of transpiration. We found that:

a) the maximum rate of stand transpiration was observed at the second shallowest site (4.3 m) rather than the shallowest (2.4 m);

b) as DGW increased from 4.3 m to 37.5 m, stand transpiration declined;

c) the smallest rate of stand transpiration was observed at the deepest (37.5 m) site;

d) there was a strong ($r^2 = 0.98$) negative linear correlation between average monthly stand transpiration and the $\delta^{13}C$ of current year's sapwood, indicative of increasing water-use-efficiency with decreasing availability of groundwater; and

e) there was no evidence of convergence in rates of water use for co-occurring species at any site.

1   We conclude that even in mesic environments groundwater can be utilised by trees. We

2   further conclude that these forests are facultatively groundwater dependent when

3   groundwater depth is < 9 m and suggest that during drier-than-average years the

4   contribution of groundwater to stand transpiration is likely to increase significantly at the

5   two shallowest groundwater sites.

6   **Key words:**   Groundwater depth; tree water-use; transpiration; groundwater

7   dependent ecosystems; ^{13}C stable isotopes

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1   **1. Introduction**

2   Demand for freshwater is increasing globally in line with increasing population size,

3   with water being required especially for human consumptive use, irrigation and other

4   industrial applications (Gleick et al., 2006). To manage limited fresh water resources

5   sustainably, demand by all sectors (e.g., environmental, municipal, agricultural; Cleverly et

6   al. 2002)) needs to be quantified and managed (Cleverly et al., 2002). However,

7   environmental water requirements have traditionally received little attention and are often

8   neglected or underestimated (Eamus et al. 2005). Allocation of water to the environment has

9   frequently been limited to an allocation of water to ensure river flows (Murray et al. 2003). It

10   is now understood, though, that environmental water requirements should include allocations

11   to wetlands, woodlands, mound springs and a myriad of ecosystems that require groundwater

12   to maintain their current structure and function (Eamus et al. 2006b).

13   Transpiration by trees can be the major pathway for discharge of water from

14   woodlands and consequently determines the hydrological balance of woodlands, exceeding

15   transpiration by grasses and shrubs (Dragoni et al. 2009; Eamus et al. 2006b; Zeppel and

16   Eamus 2008). Spatial and temporal variation in tree water-use and differences among species

17   can be explained by variation in micro-climate, and species-specific physiological and

18   structural properties, including rooting depth, hydraulic architecture, leaf area and tree size

19   (O'Grady et al. 2007; Rossatto et al. 2012; White et al. 2002; Zeppel and Eamus 2008).

20   Trees have access to two or three sources of water: a) recent rainfall in the upper soil

21   profile; b) water deeper in the profile from past rainfall events; and in some locations, c)

22   groundwater and its associated capillary fringe (Eamus et al. 2006b; Naumburg et al. 2005).

Access to groundwater can affect plant growth, survival, rate of water-use and local water budgets (Carter and White 2009; Miller et al. 2010; Zencich et al. 2002). In semi-arid Western Australia, for example, increased depth to the shallow, unconfined Gnangara aquifer over the past several decades has resulted in floristic changes including widespread mortality of native woodlands (Groom et al., 2000; Canham et al., 2009; Stock et al., 2012). However detailed assessment of seasonal and inter-annual variability in tree water-use at sites with differential access to groundwater has not been made for this or any other important municipal water source in Australia. This is in contrast to numerous studies quantifying water use in riparian forests of semi-arid south-western America (Cleverly et al., 2002; Scott et al., 2004; Nagler et al., 2005). In fact groundwater use by trees growing over shallow water tables is extensive across arid and semi-arid regions (Cleverly et al. 2006; Scott et al. 2006; Smith et al. 1998). Where groundwater-use has been identified and quantified, differences in rates of stand water-use can be explained by differences in groundwater availability, which can be inferred from groundwater depth (Baird et al. 2005; Carter and White 2009; O'Grady et al. 2007).

Generally it is assumed that transpiration decreases monotonically with increasing depth-to-groundwater (DGW) (Butler et al. 2007; Landmeyer 2012; McDonald and Harbaugh 1988). However, it is more likely that transpiration is maximised at an optimal DGW that varies by plant functional type and rooting depth (Baird et al. 2005; O'Grady et al. 2011; Zeppel 2013), but this has rarely been tested in the field. While there is little question that transpiration is smallest where groundwater is deepest (Carter and White 2009), counter-intuitive reductions in transpiration rates as groundwater becomes shallower than the optimal depth may arise from anoxia in the root zone. Altogether, groundwater-use by trees is dictated by DGW, plant functional type, and climate variability, and this results in variation in the timing and amount of groundwater dependence (Eamus et al. 2006a) at any given site.

In contrast to the many studies undertaken in arid and semi-arid regions, few have compared rates of tree water-use along a naturally occurring gradient of DGW in mesic regions (Carter and White 2009; Gazal et al. 2006; Lamontagne et al. 2005). Consequently we examined spatial and temporal patterns of transpiration in a mesic, temperate Eucalypt woodland across a naturally occurring gradient in DGW. Groundwater-use by vegetation at these same sites has been established through multiple data sets, including step changes in structural attributes (e.g. basal area, leaf area index and tree height; Zolfaghar et al., 2014), hydraulic architecture and water relations (Zolfaghar et al., 2015a, b). A single, normalised response function using 16 multiple-scale (leaf, branch, tree, stand) traits has been developed for this site which describes the impact of differences in groundwater depth on ecosystem structure and function (Eamus et al., 2015).

Our objectives in the current study were to:

1) Quantify spatial and temporal patterns in rates of stand water-use at multiple sites differing in DGW;

2) Determine whether variation in intra-specific stand water-use can be explained by variation in DGW;

3) Determine whether variation in $^{13}C:^{12}C$ ratios of stem wood can provide insight to variation in water-use-efficiency across sites differing in DGW;

4) Determine whether, during relatively dry periods, rates of transpiration will decline more at the deepest DGW sites than at shallower sites; and,

5) Compare rates of tree water use for co-occurring species at a number of sites, to establish whether convergence to a common rate of water use is apparent.

2. Material and Methods

2.1. Site description

This study reports on a detailed assessment of daily and seasonal transpiration over 16 months at four sites located across an 8.5 km transect in remnant native *Eucalyptus* woodland within the Kangaloon bore-field of the Upper Nepean catchment; 110 km south-west of Sydney, New South Wales, Australia (between 34^o29' S 150^o34' E and 34^o32' S 150^o37' E). These four sites were chosen to span a range of average DGW (2.4 m, 4.3 m, 9.8 m and 37.5 m) within the same climate regime (Fig. 1). DGW in this area has been monitored by the Sydney Catchment Authority (SCA) on a daily basis since 2006. Each experimental site was centred around a single groundwater monitoring bore, with all measurements of sapflow and leaf area index (LAI) conducted within 50 m of this bore. During the drought period 2006 – 2010 inclusive, DGW was typically 1-3 % deeper at the deepest site (37.5 m DGW) compared to the study period of 2011-2012. However for the remaining three shallower sites, DGW was 8 to 37 % deeper during the drought years than during the two wet years of this study. Nevertheless average DGW fluctuated minimally (<10%) across all sites for the period 2006 – 2012.

The study area receives a long-term average annual rainfall of 1067 mm (http://www.bom.gov.au 2000-2010). On average February is the wettest month (186 mm), while August is the driest month (51 mm). Average (2000-2012) minimal and maximal temperatures occur in July (2.7 ^{o}C) and January (24.3 ^{o}C), respectively. During the study period (2011–2012), reference evapotranspiration (ET$_0$) was estimated using the Penman-Monteith method (Allen et al. 1998). ET$_0$ was parameterised with local meteorological

measurements of daily net radiation (NRLite, Kipp and Zonen, Delft, The Netherlands), vapour pressure deficit (VPD; HMP45C, Vaisala, Helsinki, Finland), LAI and wind speed (wind sentry 03001, R.M. Young Company, MI, USA) at two metres height.

The dominant tree species were defined during field surveys of basal area as those that, when summed, accounted for > 80% of total standing tree basal area. Overall there were five dominant *Eucalyptus* species across four sites: *E. radiata*, *E. piperita, E. globoidea, E. sieberi and E. sclerophylla* (Table 1). Each site contained 2–3 dominant tree species. Structural characteristic of all four sites are presented in Table 2.

2.2. Soil moisture measurements

Volumetric soil moisture content was measured with -1 which were installed in all four sites that were instrumented with sapflow sensors (see below). These probes were buried horizontally at depths of 10 cm, 30 cm and 50 cm in sites having 2.4 m and 4.3 m DGW and at 10 cm and 30 cm in sites having 9.8 m and 37.5 m DGW. Limited numbers of sensors were available and hence there we no sensors at 50 cm in the two deeper groundwater sites (9.8 m and 37.5 m DGW).

2.3. Sapflow measurements

At each site, 10 healthy trees across two or three dominant species (Table 1) were instrumented with sapflow sensors (see below) to determine whole-tree rates of water-use. Trees were selected across a representative range of DBH (Diameter at Breast Height) to allow scaling from individual to stand scales. Measurements commenced in January 2010 (summer) at the 37.5 m DGW site and continued until December 2012 (summer). Sensors were installed at the three remaining sites between mid-2010 and September 2011 such that

1   sapflow was measured concurrently at all four sites for a 16-month period (Sept 2011–Dec

2   2012 inclusively).

3   Heat dissipation sapflow sensors (Granier 1985) were used to measure rates of tree

4   water-use. Sensors were manufactured in the laboratory of the terrestrial ecohydrology

5   research group (TERG) at the University of Technology Sydney (UTS). Three independent

6   laboratory calibrations of these sensors against transpiration rates measured in weighing

7   lysimeters were conducted and confirmed that the estimates of sapflow velocity were within

8   the accepted range of accuracy (Zolfaghar 2014).

9   Two probes were inserted radially into the stem sapwood with a vertical separation of

10   a minimum of 10 cm, wherein the upper probe was located at 1.3 m height. The upper probe

11   contained a thermocouple and electric heater that was provided with constant power (0.2 W),

12   while the lower probe contained only a thermocouple. The two temperature (T) sensors

13   measure heat dissipation from sapwood and xylem water, which increases as a function of

14   sapflow. This approach enables the measurement of xylem sapflow velocity from the

15   relationship between difference in temperature and sap velocity. When sapflow velocity is

16   zero, the temperature difference between the two sensors is maximal. Granier (1985) defined

17   a flow index (K); calculated from the measured temperature difference between the upper

18   heated sensor and the lower reference sensor (ΔT) and the maximum measured temperature

19   difference, occurring at zero flow velocity (ΔT_{max}):

20                         $$K = \frac{(\Delta T_{max} - \Delta T)}{\Delta T_{max}} \qquad \text{Eq. (1)}$$

21   The value of ΔT is determined from the differential voltage measured between the

22   upper and lower thermocouple. The following empirical relation between the value of K and

23   the actual sapflow velocity (V) was found (Equation 2; (Lu et al. 2004):

$$V = 0.0119 \times K^{1.231} \, cm/s \qquad \text{Eq. (2)}$$

In the current study, at least one additional 3-probe sensor was used in each tree. Three probes systems record the natural temperature gradient in the sapwood, which is then subtracted from the measured ΔT. The third probe was located at the same height as the heated probe, which was equidistant to both reference probes (i.e., 10 cm laterally and longitudinally). During the life of the project the sap flow sensors were inspected on monthly basis and in average every three months (could be longer or shorter according to the condition of the sensors) were replaced.

2.4. **Zero flow**

To calculate K, ΔT_{max} was determined for discrete seven-day intervals during the study period using a double regression method (Lu et al. 2004). Having established ΔT_{max} every seven days, K was calculated for each tree using Equation 1. Sap velocity was calculated using Equation 2 for each sensor (m s^{-1}). Temperature differences between sensors were measured once per minute and recorded as 10-minute averages.

2.5. Sapwood area

At each site, sapwood cross-sectional area (SA) across a range of tree sizes in each species was determined on samples that were collected using a six millimetre diameter increment corer. Two perpendicular cores were taken from each tree (8-10 trees were sampled from each species). Sapwood was distinguished from heartwood by visual inspection of a distinct colour change. When the boundary between sapwood and heartwood was not clear, sapwood was stained with Methyl orange. Sapwood depth was used to calculate SA by assuming a circular cross-section. Estimating SA was critical for scaling flow rates to whole tree and stand scales.

1   **2.6. Spatial scaling**

2   To scale transpiration rates from individual trees to the entire stand, DBH of all trees

3   within three replicate plots (20 m × 20 m) was measured at each site, from which the total

4   sapwood area per hectare of land was estimated for each species ($SA_{species}$). The average sap

5   velocity of each species in each hour ($SV_{species}$) was multiplied by $SA_{species}$ to determine

6   sapflux (J_s) (Zeppel et al. 2008):

7    $$J_S = \sum SA_{species} \times SV_{species} \quad \text{Eq. (3)}$$

8   In each 24-hour period, 10-minute J_s was summed to determine daily sapflow rates,

9   expressed as a volume (cm^3 day^{-1}) (Zeppel et al. 2006) and scaled by ground area (mm day^{-1}).

10   In those species that were not used for measurements of sapflow and which accounted for

11   less than 20% of the tree basal area of each site, J_s was estimated as the product of average

12   velocity of all trees measured at the site (SV_{site}) and $SA_{species}$. At each site, daily rates of stand

13   transpiration in each tree species were calculated by summing J_s, expressed as volume of

14   water transpired per unit ground area per day (mm day^{-1}). Stand transpiration was calculated

15   by summing the daily transpiration of all species at a site.

16   **2.7. Stable isotope analysis**

17   Tree cores (one core per tree) were collected from each of the sites with a power corer

18   at slow speed. The cores were polished with sandpaper but no distinctive tree rings were

19   observed. Due to the lack of distinctive tree rings to identify annual growth increments, slices

20   were collected from the core every 300 μm with a microtome. A total of 20-25 samples were

21   collected from the sample year sapwood of each core (i.e., a roughly six mm outer segment of

22   the core, beginning below the bark and vascular cambium). Samples were finely ground

23   using a bead mill grinder, and ~100 - 200 mg of sample was transferred into a 3.5 mm X 5

11

1 mm tin capsule. The carbon isotopic composition was measured using a Picarro G2121-i

2 analyser for isotopic CO_2.

3   The carbon isotope ratio of plant material ($\delta^{13}C$) is quantified on parts per thousand

4 basis (i.e., per mil ‰; Equation 4):

5     $$\delta^{13}C\ ‰ = (R_{sample} / R_{standard} - 1) \times 1000 \qquad \text{Eq. (4)}$$

6

7 where R is the $^{13}C /^{12}C$ isotopic ratio relative to the standard reference material (Vienna Pee

8 Dee Belemnite). Intrinsic water use efficiency (WUE_i) was calculated from Equation 5:

9     $$WUE_i = [C_a(b-\Delta^{13}C)]/[1.6(b-a)] \qquad \text{Eq. (5)}$$

10

11 where a and b are fractionation factors for CO_2 arising from discrimination against $^{13}CO_2$

12 compared to $^{12}CO_2$ during diffusion through stomatal pores ($a = 4.4‰$) and by the enzyme

13 Rubisco ($b = 27\ ‰$). C_a is the concentration of CO_2 in the atmosphere and $\Delta^{13}C$ is the

14 discrimination shown by the plant against ^{13}C arising from both the diffusional and enzymic

15 processes. There is a linear correlation between $\Delta^{13}C$ and WUE_i. $\Delta^{13}C$ was calculated from

16 Equation 6:

17     $$\Delta^{13}C = (-8 - \delta^{13}C)/(1 + \delta^{13}C/1000) \qquad \text{Eq. (6)}$$

18

19 See Farquhar et al., (1989) for further details.
20

21 **2.8. Statistical analysis**

22   The differences between SA and DBH of different species and sapflow density of all

23 species within each site for three representative days were tested using analysis of variance

24 (ANOVA). The relationship between DBH and SA and the relationship between sap velocity

1 and DBH were also tested using power function regression (Meinzer et al. 2005). Analysis of

2 covariance (ANCOVA) was used to test the null hypotheses that: 1) the regression

3 coefficients were equal to zero amongst all species; and, 2) the slope of the DBH-SA

4 relationship did not differ amongst species. For all statistical tests depth-to-groundwater was

5 considered as independent variable. Analyses were performed using IBM SPSS

6 STATISTICS (version 19, Armonk, NY, USA).

3. Results

3.1. Climate

9 Total rainfall was 1561 mm in 2011 and 1188 mm in 2012, which were 46% and 11%

10 larger than the long term average (1067 mm yr^{-1}; 2000–2010). During the 694 days that

11 measurements of sapflow were collected, rainfall was received on 415 days. Mean summer

12 and winter temperatures were 16º and 7ºC respectively. Thus the climate of these sites is best

13 described as temperate mesic with warm summers and cool winters. VPD was very low

14 (mean summer and winter VPD were 0.45 and 0.25 kPa, respectively) and generally

15 remained below 1 kPa during the experimental period (Fig. 2). It is apparent that 2011 and

16 2012 were wetter, cooler and more humid than the long-term average values.

17 Soil water content measurements during 2012 showed that the site with deepest water-table

18 (37.5 m DGW) had the lowest soil water content except a short period in early March 2012

19 (Figures shown in Supplementary data). During 2012 measurement, the site with 4.3 m DGW

20 constantly had larger soil water content (maximum of 0.61 g cm^{-3}). (Figures in supplementary

21 data).

22

23

1   *Relationships amongst DBH and sapwood area*

2   As DBH increased, SA increased in all species and across all sites (Fig. 3). The

3   relationship between SA and DBH at each site varied significantly between species except at

4   the site where DGW was 9.8 m (species × site, F = 1.106; p = 0.35; df = 2,19). Likewise, the

5   coefficient of determination (r^2) was different between species within each site except at the

6   deepest site (37.5 m DGW). Additionally, regression coefficients were significantly different

7   across sites for all species. Stem diameter explained 87–97% of variation in SA.

8   **Sapflow density**

9   The diurnal pattern of sapflow density (cm^3 cm^{-2} h^{-1}) on three representative days in

10   summer 2011–2012 (December–February) and winter 2012 (June–August) display typical

11   diurnal patterns with maximum values occurring around noon in both seasons (Fig. 4 and Fig.

12   5). Transpiration rates tended to peak earlier in the day during the summer compared to

13   winter (cf. Figs. 4 and 5).

14   Climatic conditions of the study area during the three representative days that are

15   illustrated in Figures 4 and 5 are presented in Table 3. During both seasons ET_0 and VPD

16   were consistently small. Variations in the difference between maximum and minimum

17   temperatures were larger during the summer than in the winter, but conditions were otherwise

18   relatively constant during each representative period.

19   During summer 2012 average sapflow density of the three representative days was

20   larger in the two deepest sites (9.8 m and 37.5 m DGW) than the two shallowest sites. At that

21   time, sapflow density in *E. globoidea* reached a maximum of 13.75 cm^3 cm^{-2} h^{-1} at site 37.5

22   m DGW but only 8.90 cm^3 cm^{-2} h^{-1} at site 4.3 m DGW (Fig. 4). Similarly, sapflux density in

23   *E. piperita* was largest at site 9.8 m DGW (Fig. 4). Among the two shallowest sites sapflow

1   density reached a higher peak in *E. radiata* at site 2.4 m DGW than in any of the dominant

2   species at site 4.3 m DGW. Sapflow density was smaller during winter than in the summer

3   because of the cooler temperatures and smaller VPD in winter compared to summer.

4   In summer maximum rates of average sapflow density were similar across species at

5   the 4.3 m DGW site but for the remaining three sites there was variation in maximum rates of

6   sapflow density among species (Fig. 4). Likewise, inter-specific differences in water-use

7   during winter were observed at three sites: 2.4 m DGW (larger diurnal sapflow density in *E.*

8   *radiata*), 4.3 m DGW (smaller in *E. piperita*) and 9.8 m DGW (larger in *E. piperita*) (Fig. 5).

9   On average and including nocturnal measurements, sapflow density in *E. piperita* during

10   winter was significantly smaller than for other species at site 4.3 DGW ($F=10.76$, $p<0.001$;

11   $df=2,213$). In contrast at site 9.8 m DGW, sapflow density in *E. piperita* was significantly

12   larger than in co-occurring species ($F=5.58$, $p=0.004$; $df=2,213$). In the regression analysis

13   between sap velocity and DBH, none of the derived slopes were significantly different from

14   zero ($F=0.47$, $p=0.57$; $df=1,358$), which indicates that there was not a significant effect of tree

15   size on sap velocity.

16   At site 2.4 m DGW, daily transpiration reached a maximum of 0.35 mm day^{-1} for *E.*

17   *radiata* and transpiration rate in *E. radiata* was consistently larger than in the co-occurring *E.*

18   *piperita* (Fig. 6a). Both species exhibited larger maximal daily rates of transpiration in

19   summer than winter because of the longer sunlit period, warmer temperatures and larger daily

20   average VPD in summer than winter (cf. Figs. 2 and 6a).

21   The daily rate of transpiration in *E. globoidea* growing at the 4.3 m DGW site was

22   larger than that of the other two co-occurring species (maximum 0.62 mm day^{-1}) across the

23   entire study period (Fig. 6b), and these differences were larger in summer than winter. On

average the lowest rates of daily transpiration at the site with 4.3 m DGW were recorded for *E. sieberi*, except during a short period in September 2012 when transpiration in *E. sieberi* was larger than that of *E. piperita* (Fig. 6b).

E. sclerophylla was dominant at the two sites with deeper groundwater and showed the largest transpiration rates compared to the co-dominant species at these sites. At site 9.8 DGW *E. sclerophylla* transpired a maximum of 0.46 mm day^{-1}, which was second only to the maximum rate obtained by *E. globoidea* at site 4.3 DGW (cf. Figs. 6b and 6c). By contrast, *E. globoidea* maintained the lowest transpiration rates at sites 9.8 m and 37.5 m DGW compared to the other two species at that site (Fig. 6c). At site 37.5 m DGW, *E. sclerophylla* maintained a larger transpiration rate than *E. globoidea* throughout the entire measurement period (Fig. 6d). The rate of transpiration of *E. sclerophylla* at 9.8 m DGW was approximately twice that observed at site 37.5 m DGW (Figs. 6c, 6d).

Stand transpiration was calculated by summing the daily transpiration of all species measured at each site (i.e., the sum of all species in each panel of Fig. 6). Throughout most of the period from September 2011 to December 2012, the rate of stand transpiration was largest at the 4.3 m DGW site, where peak summer and winter rates of stand transpiration were approximately 1.35 mm day^{-1} and 0.80 mm day^{-1}, respectively (Fig. 7). In contrast, the deepest site (37.5 m DGW) exhibited the smallest rates of stand transpiration across the 16-month study period, reaching peak summer and winter rates of 0.57 mm day^{-1} and 0.30 mm day^{-1} respectively (Fig. 7). The rates of stand transpiration at sites 2.4 m DGW and 9.8 m DGW were intermediate and overlapped considerably across the 16-month period: peak summer rates were 0.76 mm day^{-1} (2.4 m DGW) and 0.71 mm day^{-1} (9.8 m DGW) while winter stand transpiration was 0.42 mm day^{-1} and 0.37 mm day^{-1}, respectively.

1   Monthly site-level totals of stand transpiration followed a seasonal pattern, with larger

2   rates in summer (5 – 18 mm month^{-1}) than winter (2.5 – 12 mm month^{-1}) (Fig. 8). The largest

3   rates of monthly transpiration (e.g., 25 mm month^{-1}, October 2012) were consistently

4   observed at site 4.3 m DGW, although the difference across sites was smaller during winter.

5   Monthly total stand transpiration for all tree species present (including sub-dominant

6   trees) showed a pronounced peak at 4.3 m DGW, with rates of water-use declining rapidly at

7   deeper and shallower sites (Fig. 8). Inter-monthly variability in monthly stand transpiration

8   was largest at the 4.3 m site and smallest at the deepest groundwater site (37.5 m DGW).

9   Cumulative rainfall and stand transpiration of all tree species (including estimated

10   rates in sub-dominant species) are presented for the year 2012 (Fig. 9). Cumulative rainfall

11   during 2012 was 1188 mm. Total annual stand transpiration was largest at site 4.3 m DGW

12   (188 mm) and smallest at site 37.5 m DGW (95 mm). Between sites, differences in

13   transpiration were small during winter and increased during the dry spring and summer,

14   especially at site 4.3 m DGW where cumulative transpiration was always larger than at the

15   other sites (Fig. 9).

16   The δ^{13}C increased significantly with increasing DGW (F = 54.17, P < 0.001; Table

17   2). The largest (–27.55) δ^{13}C were measured at the deepest DGW sites. The smallest δ^{13}C was

18   recorded at the 4.3 m DGW site. The δ^{13}C of the shallowest DGW site did not conform to this

19   trend and maintained a δ^{13}C that was closer to the values recorded at the deepest sites (Table

20   2).

21   The δ^{13}C of current year sapwood was linearly correlated with average monthly rates of stand

22   transpiration (Fig. 10). The site with the largest rate of monthly transpiration (4.3 m DGW)

23   maintained the most negative δ^{13}C (and hence the smallest intrinsic water use efficiency;

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1   WUE$_i$ =43 µmol mol^{-1}) and the site with the smallest rate of monthly transpiration (37.5 m

2   DGW) had the largest (least negative) δ^{13}C of sapwood (and hence the largest intrinsic water

3   use efficiency; WUEi = 73.4 µmol mol^{-1}). Intrinsic water use efficiency for the intermediate

4   DGW sites were 66.0 and 60.3 µmol mol^{-1} for the 9.8 and 2.4 m DGW sites respectively.

4. Discussion

A strong allometric power function relationship was found between SA and DBH at all sites and for all species (Fig. 3), consistent with the results of studies across a range of different species and ecosystems (Cienciala et al. 2000; Eamus et al. 2000; Kelley et al. 2007). The relationship was sufficiently robust (r^2 = 0.77 to 0.97) to make stem diameter a reliable predictor of SA and lending confidence in our up-scaling from tree-scale measurements to stand-scale estimates of transpiration.

The results described herein identify: (i) a non-linear relationship between depth-to-groundwater (DGW) and stand-scale transpiration; (ii) an absence of convergence in inter-species differences in rates of water-use; (iii) low rates of stand-scale water-use despite access to groundwater at two sites; and, (iv) seasonal variation in rates of stand water-use. We now discuss these principal results.

Within a species, the rate of tree-scale transpiration (per unit ground area) was always larger for trees growing at a shallower groundwater site than for trees of the same species growing at the deeper groundwater site, as expected if groundwater was being utilised at these sites. As was observed with inter-specific differences in transpiration, intra-specific differences across sites were the result of larger sapwood area per tree at shallower sites than at deeper sites, while sap velocities did not differ between sites. We have already established (Zolfaghar et al. 2014) that basal area and leaf area were largest at the two shallowest sites and smallest at the deepest two sites. Given well-established relationships between water availability and rates of tree water-use (Eamus et al. 2016) we conclude that increased access to groundwater *generally* results in increased utilisation of the resource, even in mesic environments where rainfall is relatively abundant; and compared to arid and semi-arid sites.

However, this tree-scale result did not result in a simple relationship between DGW and stand-scale water-use. Stand-scale transpiration was largest at the site having a 4.3 m DGW during the study period. At this site, LAI and basal area were comparable with the 2.4 m DGW site, i.e. the shallowest groundwater site (Zolfaghar et al., 2014a). Given the similarity in structure (basal area and LAI) of the two stands at the two shallowest sites and assuming similar access to groundwater, what might explain the significantly larger rate of transpiration for the 4.3 m DGW site compared to that of the 2.4 m DGW site? We propose that this can be explained by differences in total rooting volume available at the two shallowest sites and by the development of flooding at the shallowest site. At the shallowest site (2.4 m DGW) flooding of the upper 2 m of the soil profile was evident for many months of 2011 and 2012. This results in oxygen deficits (anoxia) for roots. Oxygen stress during flooding is the result of reduced oxygen conductivity in saturated soil and has been extensively documented (Brolsma and Bierkens 2007; Rodriguez-Iturbe et al. 2007; Schuur and Matson 2001). Oxygen deficits inhibit water uptake by roots, often causing reduced stomatal opening similar to the effect of water deficits (McAinsh et al. 1996; Sojka 1992). Such impacts result in reduced rates of transpiration (Baird et al. 2005; Cleverly 2013). At the 4.3 m DGW site, flooding was not observed because the water table was deeper than at the shallowest site and consequently anoxia, reduced water uptake and reduced stomatal aperture were not evident and transpiration rates were consequently larger than at the shallowest site (Fig. 8). This is consistent with Baird et al. (2005) and Schipka et al. (2005) who also found that maximum rates of stand water use did not occur at the shallowest DGW site. In high rainfall years (as observed in the present study), the optimal depth for maximum rates of stand water-use (and therefore maximal productivity given the exchange of water for carbon through stomata), is neither the shallowest nor the deepest DGW, rather there is an optimal DGW which in this study was approximately 4 m.

Strong further support for the conclusion that groundwater utilisation was occurring at the two shallowest sites is seen in the fact that $\delta^{13}C$ of sapwood declined with increasing rates of stand transpiration, as has been observed in previous studies (Horton et al. 2001; Leffler and Evans 1999; Zhao et al. 2012). This trend in $\delta^{13}C$ across these four sites is indicative of increasing water-use-efficiency with declining water availability arising from increasing DGW (Brienen et al. 2011; Farquhar et al. 1989; Leffler and Evans 1999). The known rooting depth of *Eucalyptus* in Australia (10 m; Canadell et al. (1996), 8 m; Cook et al. (1998)) further supports our conclusion that at the two shallowest sites groundwater was utilised when soil water stores are depleted, as occurs in below-average rainfall periods. At the shallowest site, however, flooding resulted in oxygen deficits (anoxia) for roots and reduced rates of transpiration (Baird et al. 2005; Cleverly 2013). Consequently the $\delta^{13}C$ of the 2.4 m DGW site is less an indicator of the availability of groundwater for transpiration and more a reflection of the impacts of anoxia on root function.

Preceding the present study, a prolonged drought was experienced across the eastern coast of Australia (2001–2007). Groundwater access during drought at the two shallowest sites was again highly likely because of the much larger accumulation of biomass (larger basal area, tree height and LAI) at the two shallowest sites compared to the deepest sites (Zolfaghar et al. 2014), despite the occurrence of a 7-year drought. Toward the conclusion of our study period (Winter–Spring 2012), precipitation declined and stand-scale water use increased at site 4.3 m DGW due to enhancement of transpiration in *E. globoidea* (cf. Figs. 2, 6 and 10). It is common for transpiration rates to increase when evaporative demand increases (Eamus 2003) if sufficient water remains available as storage in groundwater or soil (e.g., during the dry season in tropical savannas and forests; Costa et al. 2010; Whitley et al. 2011) but not if excessive soil moisture accumulates (e.g., at site 2.4 DGW in this study) or water availability (i.e., the deepest sites, where groundwater is too deep) is limited. The linear

correlation between stable isotope composition of sapwood and monthly transpiration rate (Fig. 10) suggests that climatic conditions were closely coupled to water-use-efficiency, stomatal function and moisture availability (Eamus et al. 2013). During the relatively drier period towards the end of our study, the rate of transpiration did not increase at sites with deep groundwater (Figs. 6, 7 and 10), consistent with the hypothesis that transpiration would be more inhibited at sites with deep groundwater. During prolonged drought, VPD will increase and soil moisture content will decrease sufficiently (i.e., flooding to cease) for transpiration to also be enhanced at the site with 2.4 m DGW.

Large differences in rates of transpiration were found between co-occurring species at all sites except the shallowest site (Fig. 6). This contrasts with the convergence in transpiration rates across species at a single site that is commonly observed (O'Grady et al. (1999); Zeppel and Eamus (2008); Kelley et al. (2007)). Differences in transpiration between species in mixed stands can be due to species-specific differences in several factors, including water-use strategies (Bowden and Bauerle 2008; Bugmann 2001; Dierick and Hölscher 2009), optimal DGW (Baird et al. 2005; Cleverly et al. 2006), responses to stress (Cleverly et al. 2002), or cumulative sapwood area density (per hectare) (Jonard et al. 2011; Kumagai et al. 2007; Vertessy et al. 1997; Wullschleger et al. 2001). In our study, species-specific differences in sap velocity were much smaller than that of stand-level transpiration (cf. Figs. 3–5). The relative contribution of each species to stand level transpiration was largely driven by species-specific relativities in total sapwood area per unit of ground area rather than species-specific differences in sap velocity, in agreement with the study of Jonard et al. (2011).

Total stand transpiration at all sites was low compared with some previous studies. The maximum rate of canopy transpiration observed in the current study was 1.34 mm day^{-1}

at site 4.3 m DGW, which is considerably smaller than the maximum canopy transpiration in some Australian woodlands (Carter and White 2009; Forrester et al. 2010; Zeppel 2006) but is comparable to those observed in other Australian studies (Macfarlane et al. 2010; Mitchell et al. 2009; Roberts et al. 2001; Yunusa et al. 2010). Similarly low stand transpiration rates (1.7 mm d^{-1}) have been observed in a temperate woodland receiving high annual rainfall (3482 mm) in New Zealand (Barbour et al. 2005) and in European woodlands (Wullschleger et al. 2001). The relationship between evaporative demand and sap velocity has been examined extensively for different species and environments (Rosado et al. 2012; Schipka et al. 2005; Zeppel et al. 2004). The low sap velocities observed in the present study in winter can be partially explained by low VPD, low temperature and short day length, which result in low solar radiation input and very low evaporative demand of the atmosphere. Sap velocity for all sites was higher during summer, but still lower than expected for these woodlands. Because of high levels of rainfall, extensive cloud cover and low VPD during the 19-month study, transpiration from all four sites was frequently energy limited. Energy limitations are common in maritime and mesic environments, that is, where P exceeds reference evapotranspiration (which is a function of VPD, solar radiation and aerodynamic conductance; Cleverly et al. 2013a; Cleverly et al. 2013b; Donohue et al. 2009; Moore et al. 2008).

In conclusion, we examined the water use characteristics of mesic forests along a gradient of DGW in southeastern Australia. It was assumed that over-storey transpiration would be a major component of the water balance, but total tree transpiration from canopies was small: ranging from 9% of annual rainfall at a site with 37.5 m DGW to 16% at a site with 4.3 m DGW. The small contribution of over-storey transpiration to the water balance indicates that other pathways for discharge of rainfall contributed significantly to the water balance of the sites (Baldocchi and Ryu 2011). Large amounts of rainfall, small VPD, energy

limitations and consequentially small rates of ET_0 imply that the balance of the discharge at these sites was from runoff, except at the site with the shallowest groundwater (site 2.4 m DGW) where transpiration by trees was limited by inundation. Thus, we found the DGW at which transpiration was maximal (i.e., optimal DGW) to be $4 - 4.5$ m deep, which implies that these forests are facultatively groundwater-dependent and could be modelled as such (Baird et al. 2005). Future droughts are thus expected to reduce differences in annual transpiration between the two shallowest sites (2.4 m and 4.3 m DGW).

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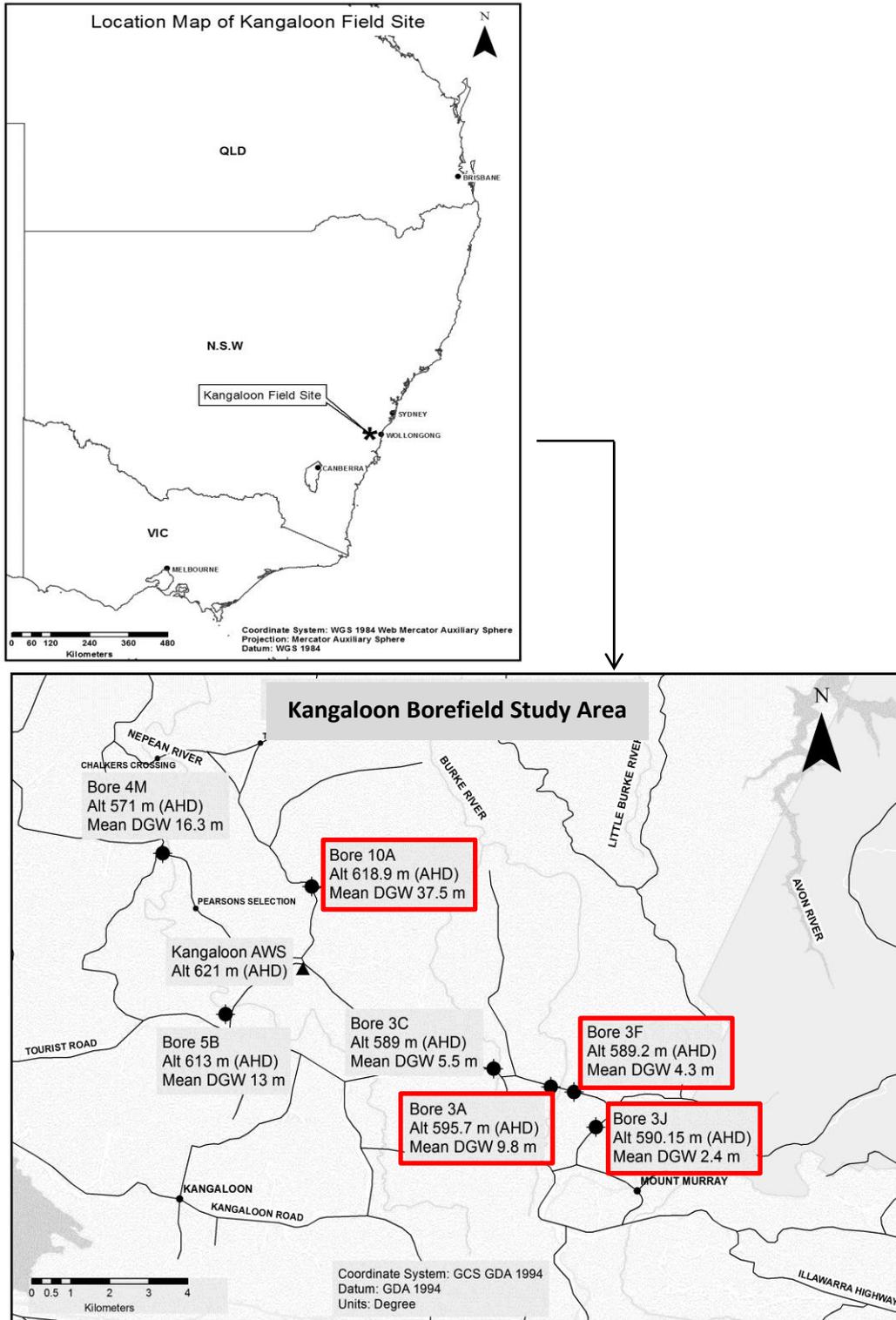
Figure 1: Study area; location of site within Australia (Top panel) and location of bores (lower panel).
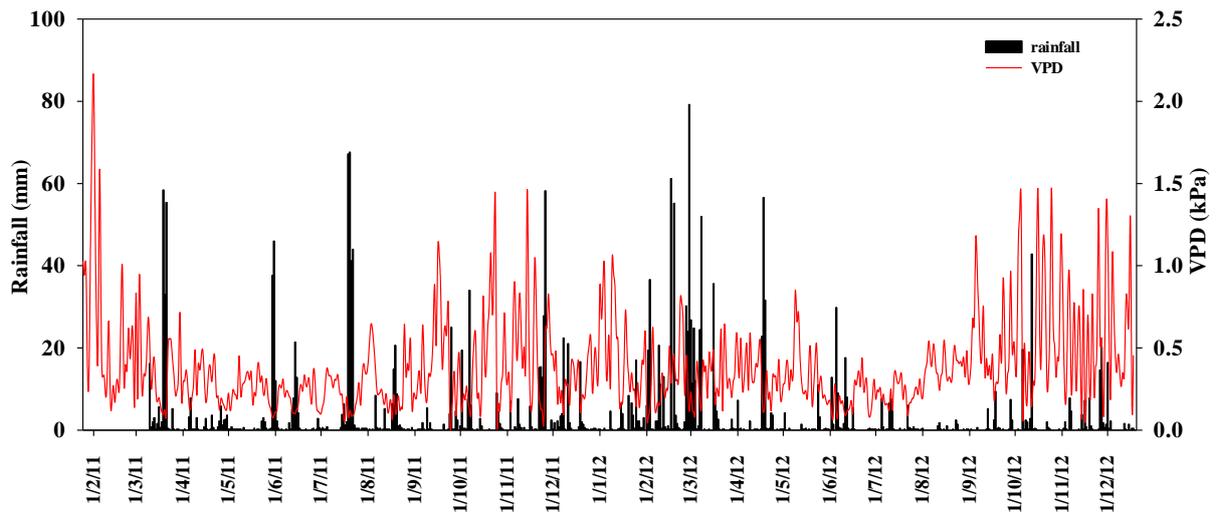
Figure 2: Daily rainfall (bars) and vapour pressure deficient (red line) over the 2 year study period.

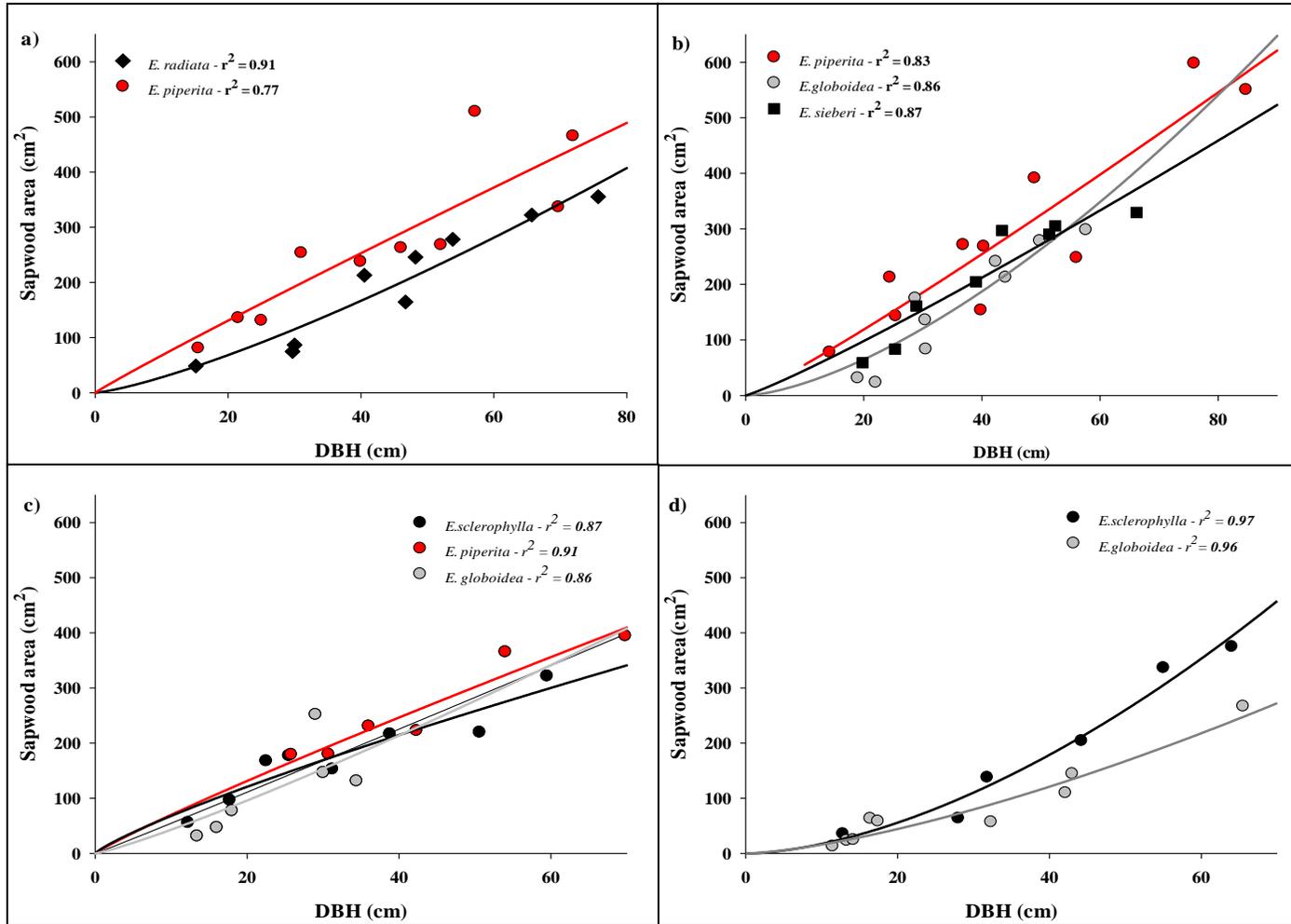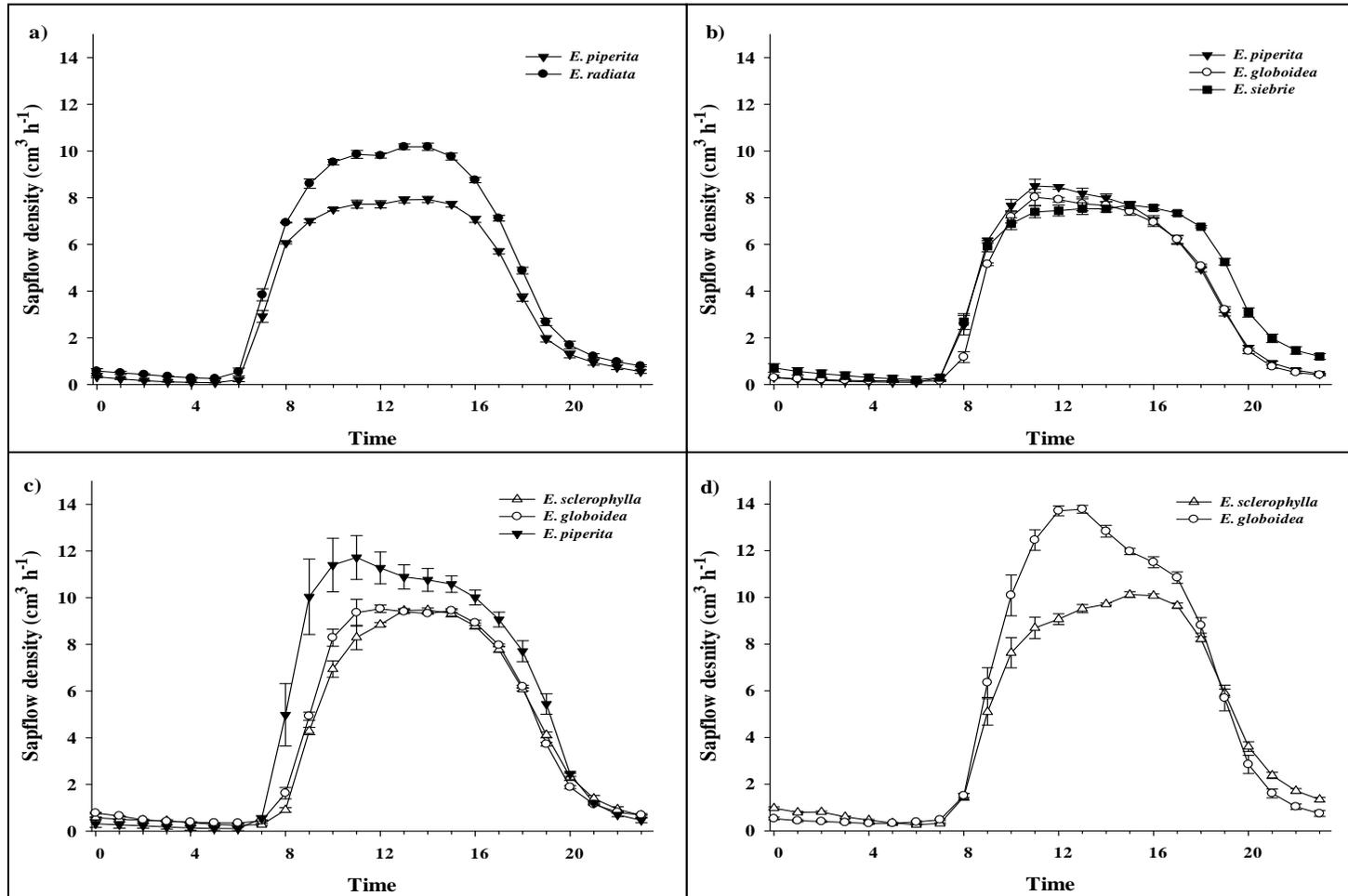**Figure 3:** The relationship between DBH (cm) and sapwood area (cm^2) for individual species growing at the four study sites: a) 2.4 m, b) 4.3 m , c) 9.8 m and d) 37.5 m depth-to-groundwater. Each point represents one tree.
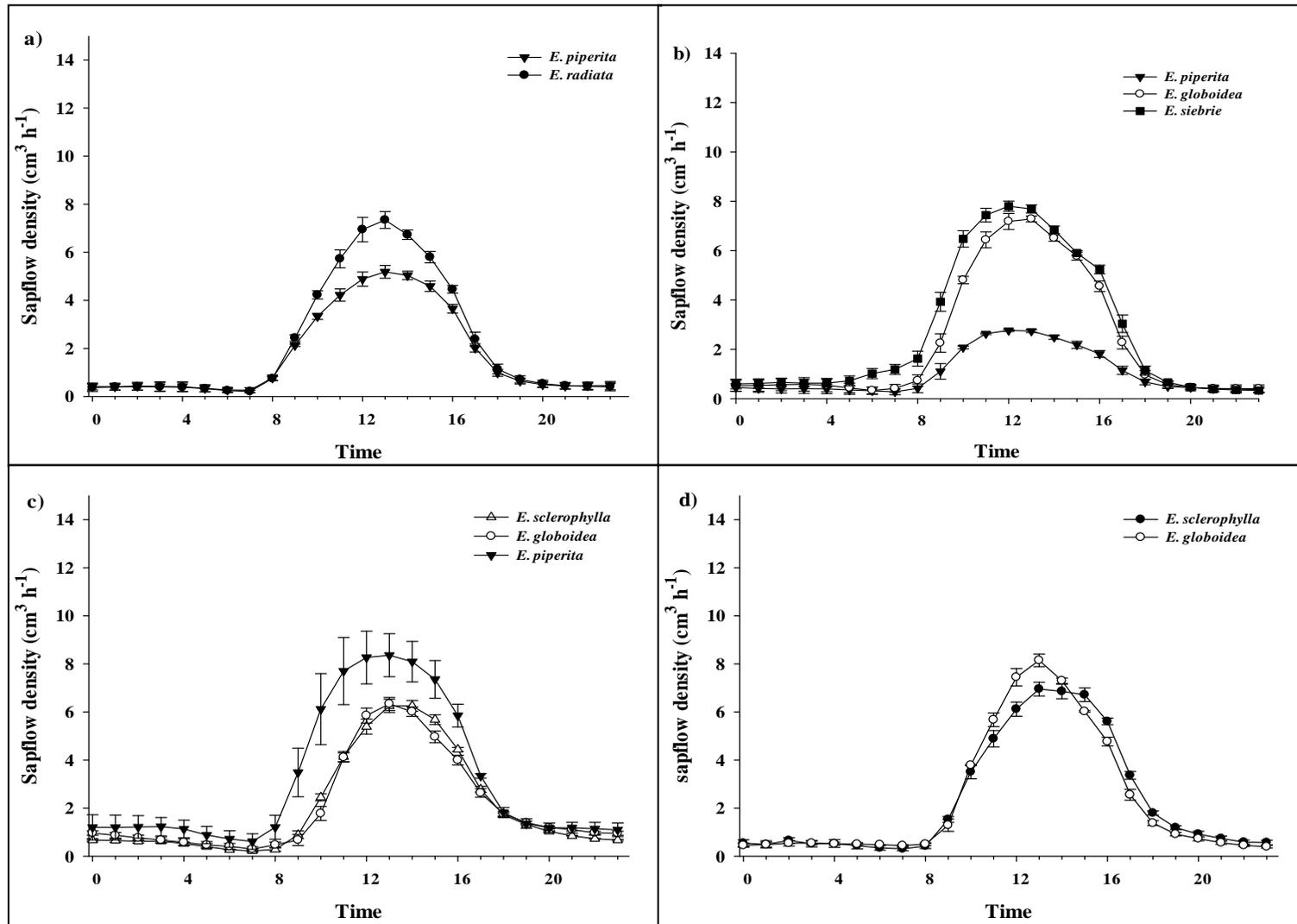
Figure 4: Diurnal patterns of water- use of each tree species for the 4 sites a) 2.4 m, b) 4.3 m, c) 9.8 m and d) 37.5 m depth-to-groundwater); 3 consecutive representative days in summer 2012 (Dec) Symbols represent mean sap flow density recorded on all trees of a species ± Standard error of mean (SE).
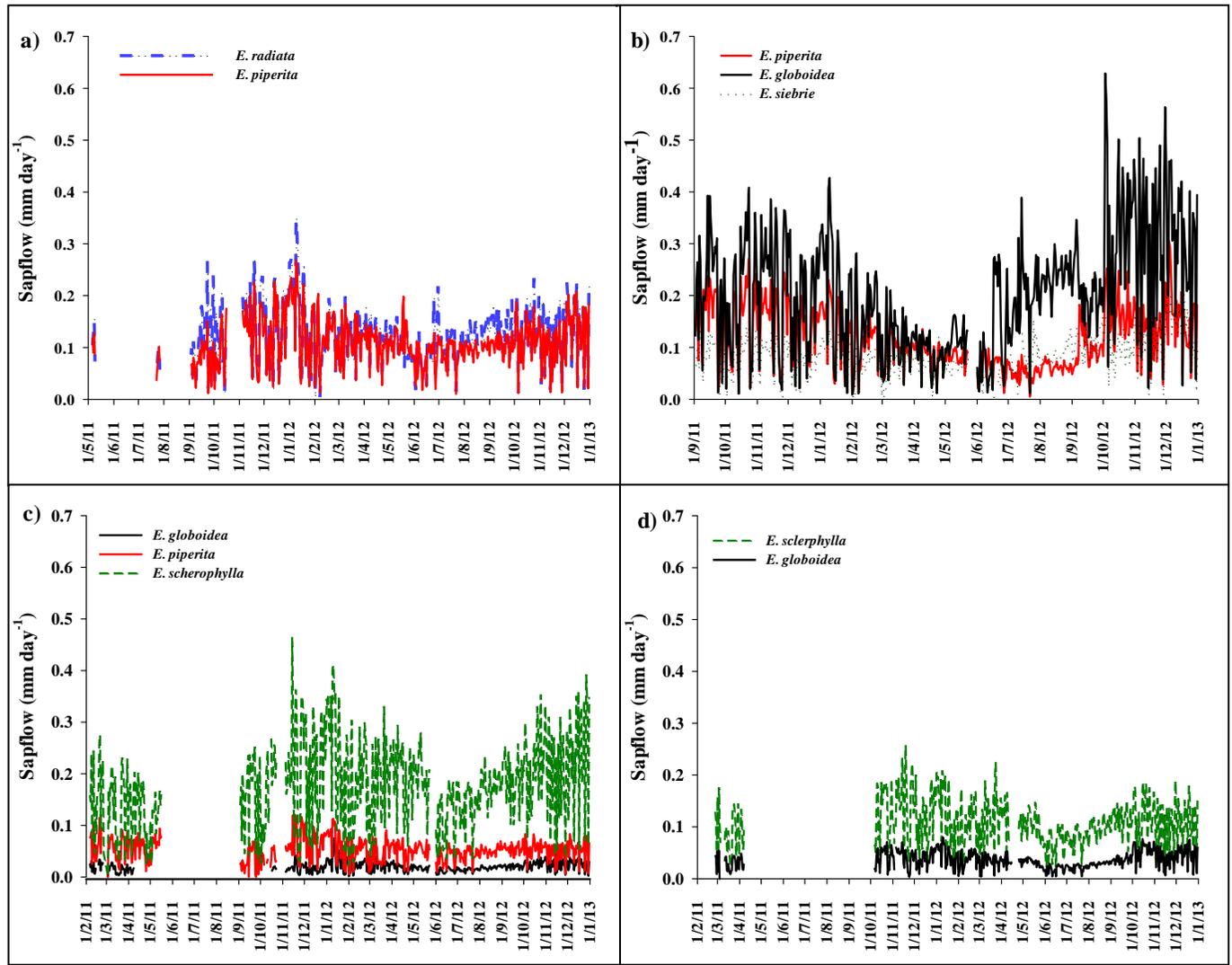
Figure 5: Diurnal patterns of water- use of each tree species for the 4 sites: a) 2.4 m, b) 4.3 m, c) 9.8 m and d) 37.5 m depth-to-groundwater); 3 consecutive representative days in winter 2012 (Jul). Symbols represent mean sap flow density recorded on all trees of a species ± Standard error of mean (SE).
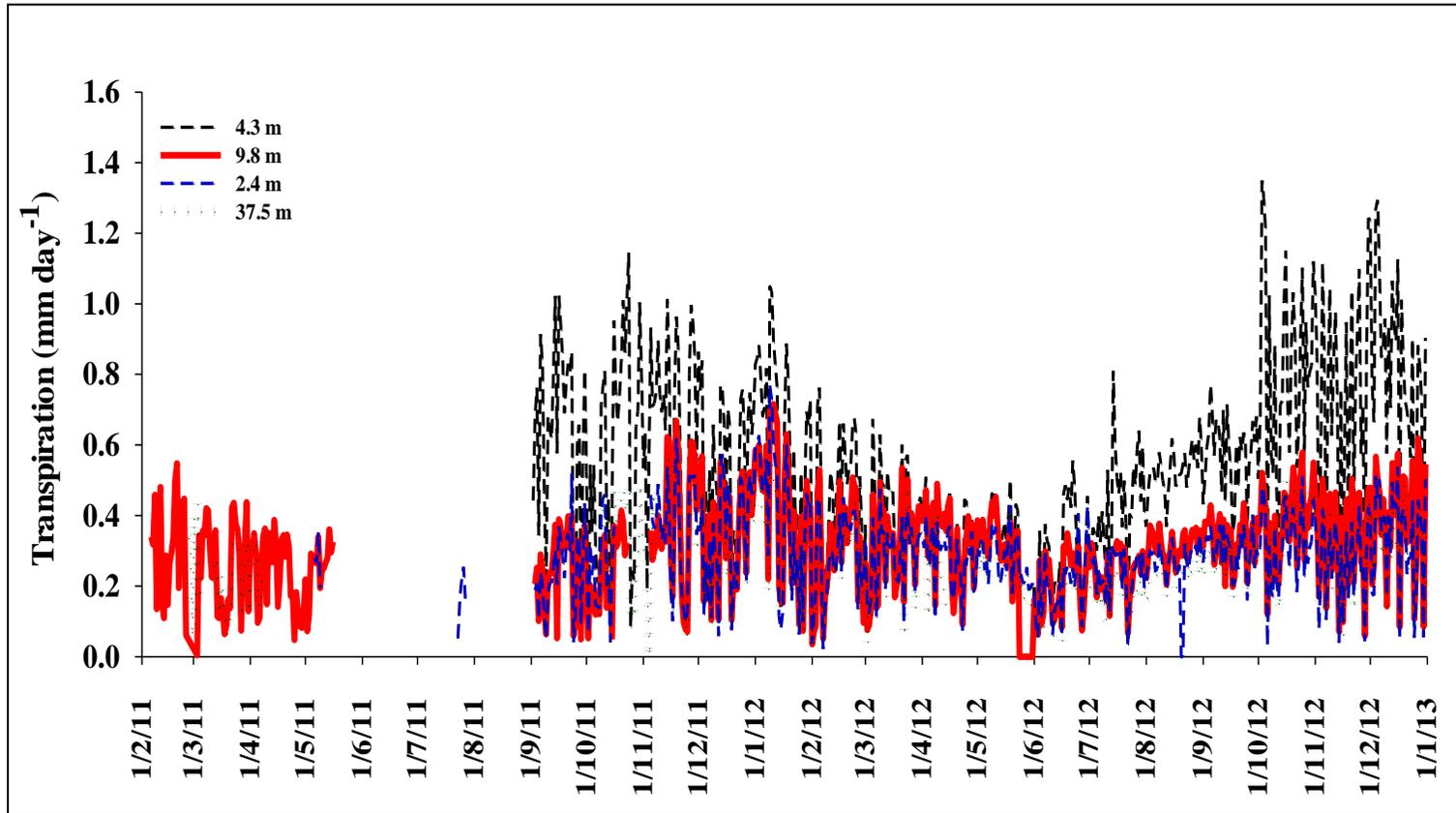
33

Figure 6: Daily sums of the rate of water- use for each species scaled individually within a stand for the study period for sites a) 2.4 m, b) 4.3 m, c) 9.8m and d) 37.5 m de depth-to-groundwater. (Missing data indicate periods of power supply or instrument failure).

Figure 7: Daily stand transpiration of the four study sites based only upon the species sampled for sapflow, (missing data indicate periods of power supply or instrument failure). Monthly water- use (mm per month) of all tree species sampled at each site.
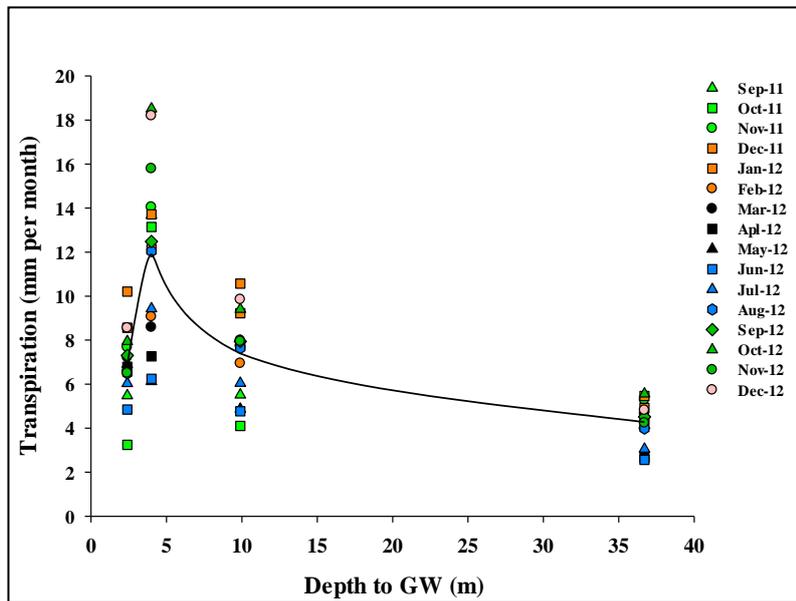
Figure 8: Monthly transpiration for all species present at each site as a function of depth-to-groundwater (m).
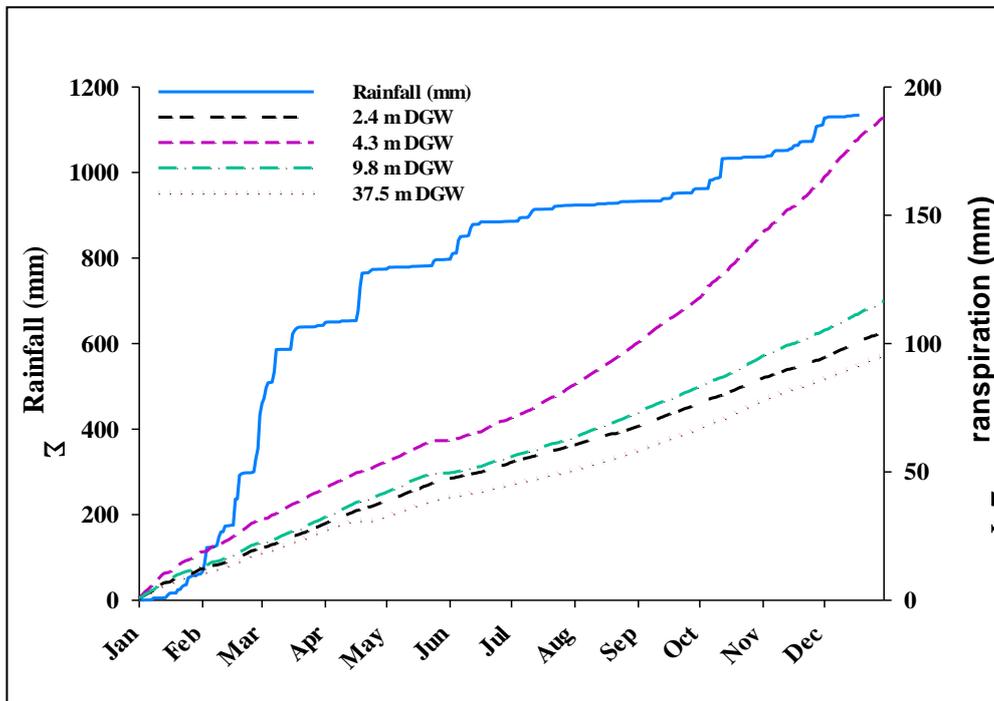
Figure 9: Cumulative stand transpiration at each site (all tree species present included) and rainfall in 2012.

1

2

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Average monthly transpiration rate (mm / month)
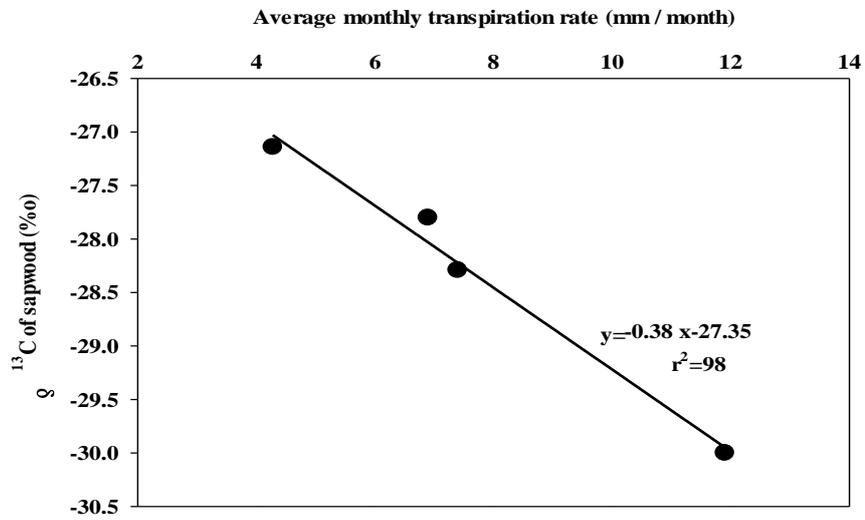

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14 **Figure 10:** A strong linear correlation between $\delta^{13}C$ of sapwood and average monthly
15 transpiration rate for four sites across a natural gradient in depth-to-groundwater.

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