

Tropical tree water use under seasonal waterlogging and drought in central Cambodia



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SUMMARY

In central Cambodia, rapid growing non-endemic species are planted for future timber production. However, less is understood about the impact of the introduction of non-endemic species on the transpiration characteristics of the forest, which has been composed of native species that adapted to the highly seasonal environments. Sap flux of two native and one non-endemic tree species in central Cambodia was measured to reveal its seasonal trends and variability in the Monsoon Asia region. Measurements were carried out in a 10- to 15-year-old forest in the dry and rainy seasons that were defined by differing rainfall patterns. The seasonal trend in depth to water table differed from that of rainfall; groundwater table depth reached zero late in the rainy season and increased gradually after the onset of the dry season. The ratio of sap flux to an equilibrium evaporation condition of the native species, Popel (*Shorea roxburghii*), showed a sharp decline at the end of the dry season, whereas that of a non-endemic species, eucalyptus (*Eucalyptus camaldulensis*), decreased in the mid rainy season while Tbeng (*Dipterocarpus obtusifolius*) did not show a clear trend. The ratio of sap flux to an equilibrium evaporation was negatively correlated with the depth to water table in Popel, but was positively correlated in eucalyptus, possibly because of the negative effects of flooding. In addition to the large seasonal variation, intra-species variation in sap flux was also large and was a major controlling factor for tree-level water uptake at this young forest site in both dry and rainy seasons. In conclusion, the transpiration characteristics of this forest were species-specific and were controlled more by the fluctuating depths to groundwater rather than the onset of the rainy/dry seasons defined by rainfall events.

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1. Introduction

Monsoon Asia experiences seasons of contrasting precipitation, i.e., a rainy season and a dry season with long periods of dry days without rain. Seasonal trends in transpiration rate are thought to differ among trees and sites because of the site-specific

environmental conditions (Tanaka et al., 2003, 2004, 2008) and species-specific ecophysiological traits (Kelliher et al., 1995; Eamus et al., 2001; O'Grady et al., 2006, 2009), which have evolved to minimize the risk of excessive water loss and physiological damage during the dry season (e.g., Law et al., 2001; McDowell et al., 2008). Transpiration and its relationship with species and environmental conditions has been intensively investigated in seasonally drought-affected regions owing to the possible threat to local water resources from plantations of fast-growing species (Calder et al., 1993; Hornbeck et al., 1993; Mielke et al., 2000; Bruijnzeel, 2004; Whitehead and Beadle, 2004).

Transpiration in the dry season is strongly influenced by the trees' access to the water source deep underground (Pinker et al.,

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1980; Tanaka et al., 2004; Kume et al., 2007). If trees have non-limiting water access in the dry season (Meinzer et al., 1999; Eamus et al., 2000; Hutley et al., 2000; Prior et al., 2004; Zeppel et al., 2004; Cleverly et al., 2006; Fisher et al., 2006; O'Grady et al., 2006, 2009; Pfautsch et al., 2011), the transpiration rate is not reduced in the mid dry season and reaches the annual maximum under the highest atmospheric evaporative demand in the dry season (Tanaka et al., 2003). However, access to groundwater does not ensure unlimited water use (Teskey and Sheriff, 1996; Franco, 1998; Meinzer et al., 1999; Leuning et al., 2005). On the Indochina Peninsula, the relationship between transpiration and tree access to groundwater sources was investigated in the montane region of Thailand (Tanaka et al., 2004), where appreciable base flow conditions are observed in the stream even in the mid dry season and the deep soils offer access to water for overlying trees (Tanaka et al., 2003, 2004). If a given tree species introduced to or removed from a stand has higher water uptake than other stand species of similar size, changes in forest species composition due to afforestation or logging could cause changes in stand-level transpiration. Similarly, if the introduced species reduces its transpiration in dry periods while other species do not, stand-level transpiration could be influenced by changes in species composition. In the central Cambodia plain information on deep soil water sources is lacking and, correspondingly, knowledge of the influence of soil water variations on tree transpiration is limited. Therefore, *in situ* measurements are required for the evaluation of forest transpiration in this region.

In this study, we measured the atmospheric evaporative demand (equilibrium evaporation, E_{eq} , Table 1), soil water environment (soil water content and depth to water table) and sap flux of three tree species in the dry and rainy seasons in central Cambodia. The objective of the study was to address the following three questions. First, what are the seasonal trends in soil water environment, precipitation and sap flux? Second, does sap flux decline in the dry season because of soil drought or simply track the seasonal trends of evaporative demand? Third, are there inter-species differences in the seasonal trends of sap flux in response to the variable environment that reflect species-specific ecophysiological traits?

2. Materials and methods

2.1. Study site

The study was carried out at the Svay Bakav water cycle study site (11°59'20"N, 104°44'27"E), Kampong Chhnang province, Cambodia. In March 2008, the site was located in a reforested area, which was established on heavily degraded land in 1998. The Cambodian government designated the area as 'community forest', which is managed by the villagers for the purpose of forest

conservation. Community forests are used by villagers for the production of non-timber forest products and timber cutting is forbidden.

The forest is composed of 10 woody species, with basal area 8.62 m² ha⁻¹ and mean tree height 10.8 m. We studied two native species, Tbeng (*Dipterocarpus obtusifolius* Teijsm. ex Miq.) and Popel (*Shorea roxburghii* G.Don.), and one artificially introduced non-endemic species, eucalyptus (*Eucalyptus camaldulensis* Dehnh.), which accounted for 19.8%, 27.7% and 13.4% of the total basal area of the stand, respectively. These species are evergreen broadleaved trees according to the observations by the villagers and Williams et al. (2008). Litter fall data showed a peak in leaf fall occurred in February to April. However, a decline in leaf area index (LAI) in these months was not detected by the periodic LAI monitoring (Fig. 1e). For eucalyptus, Popel and Tbeng, seven trees of each species were selected for sap flow measurements (Table 2). An additional non-endemic species, acacia (*Acacia auriculiformis* A.Cunn. ex Benth.), was also monitored. However, because of its narrow sapwood area, sap flux was not successfully measured and hence was not included in our analysis.

The climate at the study site is a typical Monsoon Asian climate (Tanaka et al., 2008), with a distinct dry season for 4–5 months (from the end of November to early–mid April) and a rainy season (from the end of April to November), in which nearly 90% of the annual precipitation falls. The annual precipitation in this region is 1700–1800 mm and the annual average air temperature is 23.7°, which was measured at a weather station 23 km east of the study site without major topographical changes between them (SCW, 2006). In this study site, the daytime air temperature reaches the annual maximum in March and April (33.7 ± 0.7 °C for the hottest months in 2008–2011), and the annual minimum in December and January (29.1 ± 0.9 °C for the coldest months in 2008–2011). The soil of this region is a red-yellow podzol (SCW, 2006). In the 0–3 m depth at the study site, the soil is a sandy soil with less silt and clay soil.

A weather station for the study site was established in an open site in April 2008 equipped with a pyranometer (LP PYRA 03, Delta Ohm, Padua, Italy), photosynthetically active radiation (PAR) sensor (PAR-02, Prede Co., Ltd., Tokyo, Japan), rainfall gauge (TK-1, Takeda Keiki Co., Ltd., Tokyo, Japan) and air temperature–humidity sensors (HMP45D, Vaisala, Helsinki, Finland). An anemometer (Model 05305, R.M. Young, Traverse City, MI, USA) monitored wind speed and direction. Volumetric soil water content (θ_{soil}) was monitored using time domain reflectometry (TDR) sensors (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK), which were installed at soil depths of 10, 20, 80 and 100 cm. A groundwater-level meter (HM-900-02-10, Sensez Co., Ltd., Tokyo, Japan) was installed in an observation well. Sensors were connected to a data logger (CR1000, Campbell Scientific, Logan, UT, USA), which collected data every 10 s. Averages were recorded at 10 min intervals except for rainfall, which was recorded as pulse counts.

LAI (m² m⁻²) was periodically measured for each tree selected for sap flow measurements from March 2009 at 3- to 4-month intervals using a fish-eye lens (FC-E8, Nikon Corporation, Tokyo, Japan) attached to a digital camera (CoolPix 990, Nikon Corporation). One to three hemispherical photographs were taken at fixed points below the canopy of each tree and were used for calculation of LAI with HemiView canopy analysis software version 2.1 (Delta-T Devices, Cambridge, UK). Because the stand is a mixture of several species, the calculated LAI of each tree represents the LAI of the tree and the surrounding overstorey trees, except for Tbeng, which formed a relatively monospecific stand.

Because of technical problems, monitoring of rainfall from April to October 2010 was not successful (Fig. 1). We could not obtain data for depth to water table from July 2008 to April 2009, and soil water content sensors failed periodically.

Table 1
List of abbreviations.

| Abbreviations | Unit | |
|---------------|--------------------------------------|---|
| A_s | m ² | Sapwood area |
| dbh | cm | Diameter at breast height |
| ΔT | °C | Temperature difference between heater and reference sensors |
| E_{eq} | mm day ⁻¹ | Equilibrium evaporation |
| F_d | g m ⁻² s ⁻¹ | Sap flux measured by a sap flux sensor |
| J_s | mm day ⁻¹ | Sap flux weighted by the sapwood area |
| LAI | m ² m ⁻² | Leaf area index |
| PAR | μmol m ⁻² s ⁻¹ | Photo synthetically active radiation |
| Q_{soil} | | Volumetric soil water content |
| R_n | MJ m ⁻² day ⁻¹ | Net radiation |
| SLA | m ² g ⁻¹ | Specific leaf area |
| VPD | kPa | Atmospheric vapor pressure deficit |

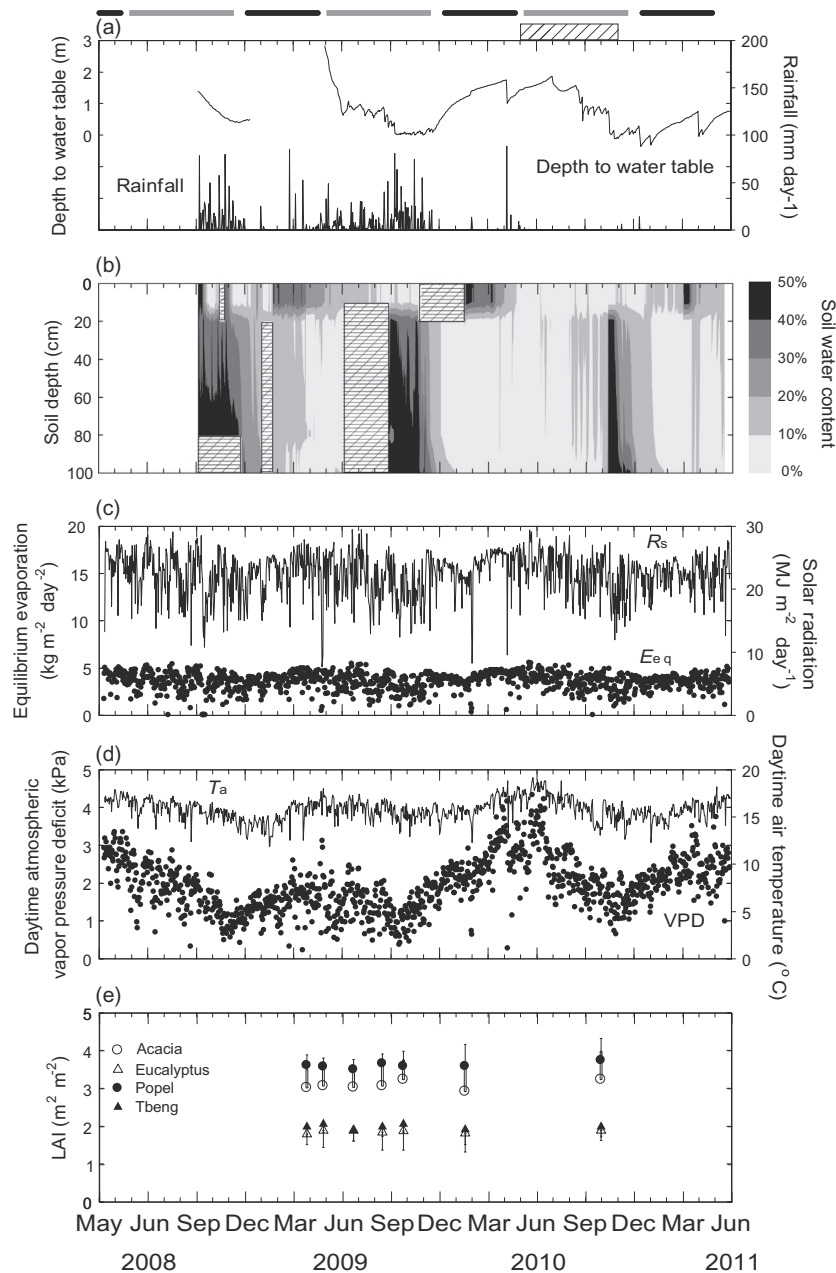


Fig. 1. Meteorological data recorded at Svay Bakav for (a) rainfall and groundwater table depth, (b) profile of soil water content, (c) short-wave radiation (R_s) and equilibrium evaporation (E_{eq}), (d) daytime atmospheric vapor pressure deficit (VPD) and air temperature (T_a), and (e) leaf area index (LAI) of each species. Black bars at the top of the figure indicate the rainy seasons, gray bars indicate the dry seasons. Periods lacking a bar are ambiguous periods when the amount of rainfall differs annually. Hatched areas indicate the periods (a and b) and depth (b) for which data are lacking because of technical problems. In (e), vertical bars represent the standard deviation ($n = 7$).

2.2. Sap flow measurements

Sap flux (F_d ; $\text{g m}^{-2} \text{s}^{-1}$) was monitored using Granier-type sap flux sensors (Granier, 1987) at breast height. Here we briefly describe the measurement system. Each sensor consists of a pair of probes 20 mm in length (heater probe and reference probe) that are inserted into the stem and measure F_d . The heater probe emits heat of a known power (0.2 W) and measures temperature, whereas the reference probe, which is set 15–20 cm below the heater probe, only measures temperature. Each sensor was connected to a four-line cable. Two of the lines connected the heater in the heater probe to a power board and the other two lines connected the thermocouple to the data logger to measure the temperature difference between the probes. To avoid the effects of solar

radiation on the temperature data measured by the sensor, each sensor was shielded by an aluminum cover and a heat insulator. Sensors were installed in April 2008 in the selected trees of each of the three species (Table 2). The difference in temperature between the heater probe and reference probe (ΔT) was monitored and used for calculation of F_d (Granier, 1987). Two data loggers (CR1000, Campbell Scientific) with attached multiplexers (AM16/32, Campbell Scientific) scanned ΔT at 10 s intervals and the average was recorded at 30 min intervals.

Two to three sensors were installed in each tree to take into consideration the circumferential variation in F_d for calculation of the mean F_d of each tree. Sensors were installed at random aspects on the trunk (i.e., radial positions on the trunk relative to compass direction) in order to avoid the effects of bias of F_d in a certain

Table 2
Description of the studied trees.

| Tree | dbh (cm) | Leaf area ^a (m ²) | Apwood area ^b (cm ²) |
|--|----------|--|---|
| <i>Eucalyptus</i> | | | |
| Sapwood area = 6.15dbh – 31.0, $r^2 = 0.823$ | | | |
| 1 | 8.8 | 0.60 | 23.08 |
| 2 | 8.7 | 0.58 | 22.46 |
| 3 | 12.9 | 1.27 | 48.28 |
| 4 | 16.5 | 2.49 | 70.40 |
| 5 | 15.5 | 2.07 | 64.26 |
| 6 | 18 | 3.28 | 79.62 |
| 7 | 24.4 | 10.76 | 118.96 |
| <i>Popel</i> | | | |
| Sapwood area = 8.12dbh – 67.5, $r^2 = 0.671$ | | | |
| 1 | 14.5 | 5.73 | 50.17 |
| 2 | 14.8 | 6.04 | 52.60 |
| 3 | 14 | 5.25 | 46.11 |
| 4 | 11.4 | 3.34 | 25.01 |
| 5 | 15.2 | 6.47 | 55.85 |
| 6 | 14.2 | 5.44 | 47.74 |
| 7 | 12 | 3.70 | 29.88 |
| <i>Tbeng</i> | | | |
| Sapwood area = 6.22dbh – 34.8, $r^2 = 0.914$ | | | |
| 1 | 15.4 | 4.71 | 61.05 |
| 2 | 10.9 | 1.93 | 33.04 |
| 3 | 12 | 2.40 | 39.89 |
| 4 | 12.3 | 2.55 | 41.75 |
| 5 | 8.7 | 1.25 | 19.35 |
| 6 | 10.2 | 1.68 | 28.68 |
| 7 | 10.5 | 1.78 | 30.55 |

^a Leaf area was obtained using an allometry equation, which was established using the nearby trees ($n = 5$).

^b Sapwood area was obtained by sapwood area-sbh relationship, which was established by injecting dye solution into the cut end of the stem of nearby trees of each species ($n = 5$).

aspect on the calculation of tree mean F_d (Tsuruta et al., 2010). Because the sapwood area was narrow and less than 30 mm in depth from the bark, we assumed that each sensor (20 mm in length) covered the whole range along the radial profile of the sapwood. The sensors were checked periodically for breakage. In cases of sensor breakage, which occurred every 6–12 months, mainly because of mechanical damage by ants and rats, the broken sensor was replaced with a new sensor.

Sap flux density (J_s ; $g\ m^{-2}\ s^{-1}$) was weighted by the sapwood area for each selected species using the formula of Kumagai et al. (2007):

$$J_s = \frac{\sum_{i=1}^7 A_{s,i} \cdot F_{d,i}}{\sum_{i=1}^7 A_{s,i}} \quad (1)$$

where $A_{s,i}$ and $F_{d,i}$ are the sapwood area and mean F_d of sample tree i , respectively. The stand-scale transpiration rate was calculated for each species as:

$$\text{Stand-scale transpiration rate} = J_s \cdot \text{total sapwood area/plot area} \quad (2)$$

In August 2009, a water-soluble dye (safranin) solution was injected into the cut end of the stem of trees of each species near the study site ($n = 5$ per species) to visualize the sap wood area in transverse section. After injection, the trees were felled to linearly regress sapwood area (A_s ; m^2) with diameter at breast height (dbh) for estimation of the daily transpiration rate by a single tree (tree water uptake, $kg\ tree^{-1}\ day^{-1}$) without destruction (Table 2).

$$\text{Tree water uptake} = \text{mean } F_d \cdot A_s \text{ of the tree} \quad (3)$$

The felled trees were used for establishment of allometric equations for estimation of leaf mass–dbh relationship (Table 2). Tree-level leaf mass was converted to leaf area by multiplication with

the specific leaf area (leaf area/leaf dry mass, SLA; $m^2\ kg^{-1}$), which was calculated from sampled individual leaves:

$$\text{Tree-level leaf area} = (\text{Tree-level leaf mass}) \cdot \text{SLA} \quad (4)$$

The atmospheric evaporative demand was represented by the equilibrium evaporation ($kg\ m^{-2}\ s^{-1}$; Jones, 1992):

$$E_{eq} = R_n / \lambda (\varepsilon + 1) \quad (5)$$

where R_n is the net radiation ($W\ m^{-2}$), ε is the ratio of the psychrometric constant ($Pa\ K^{-1}$) to the slope of saturated vapor pressure curve ($Pa\ K^{-1}$), and λ is the latent heat for water vaporization ($J\ mol^{-1}$). R_n was calculated using the measured solar radiation (R_s ; $W\ m^{-2}$) and the R_n – R_s relationship, which was established in a similarly sparse, 5-year-old rubber plantation in Kampong Cham province, central Cambodia, in September and October, 2009 ($R_n = 0.82R_s - 20.14$, $r^2 = 0.99$; TW Giambelluca and RG Mudd, University of Hawai'i at Manoa, unpublished data). We used E_{eq} rather than Penman's potential evaporation (Penman, 1948) because the leaf surface is highly decoupled from the external atmosphere (McNaughton and Jarvis, 1991) in the selected species at the study site (Miyazawa et al. unpublished data) and the risk of overestimation of atmospheric evaporative demand at the leaf surface. The ratio of J_s to E_{eq} was calculated to enable comparison of the sap flux in different seasons by elimination of the seasonal variation in evaporative demand (Santiago et al., 2000), similar to the Priestley–Taylor coefficient (evapotranspiration rate/ E_{eq}) (Priestley and Taylor, 1972).

3. Results

3.1. Soil water environment and precipitation

The mean annual daytime air temperature during the monitoring period (March 2008 to May 2011) and annual precipitation from September 2008 to September 2009 were 27.2 °C and 1777 mm, respectively. Rainfall patterns showed a distinct dry season with less frequent rainfall events (December–March) and a rainy season (April–November; Fig. 1a). In 2008–2009, the depth to water table increased to 3 m in the dry season and decreased to 0 m at the end of the rainy season (Fig. 1a). The onset of the decrease in depth to water table in 2010 (April) differed from that in 2009 (August), which indicated that large interannual variation in groundwater dynamics existed. Similarly, the annual maximum depth to water table was 2 m in 2010 and only 1 m in 2011.

Volumetric soil water content (θ_{soil}) was high in the mid rainy season and did not show a clear profile trend (Fig. 1b). Despite the rising groundwater levels at the beginning of the rainy season, the soil water content in the upper soil column (0–1 m) does not increase, presumably due to the low water retention of the sandy soil (Fig. 2). After the depth to water table decreased to less than 1 m, θ_{soil} increased rapidly, consistent with the decreasing groundwater table depth. At the study site, E_{eq} was 1316 $mm\ year^{-1}$ and 1308 $mm\ year^{-1}$ in 2008 and 2009, respectively, did not show a clear seasonal trend, and showed large day-to-day variation in the rainy season (Fig. 1c). Hereafter, we define the period in which the depth to water table was less than 0.5 m, i.e. when the surface soil layer was influenced by the groundwater table, as the water-logged period.

The daytime air temperature was low at the beginning of the dry season (December and January) and peaked at the end of the dry season and beginning of the rainy season (March and April; Fig. 1d). The daytime atmospheric vapor pressure deficit (VPD; kPa) showed a similar seasonal trend, with low values towards the end of the rainy season (September–November 2009; 1–1.5 kPa) and peaks at the end of the dry season (March–April

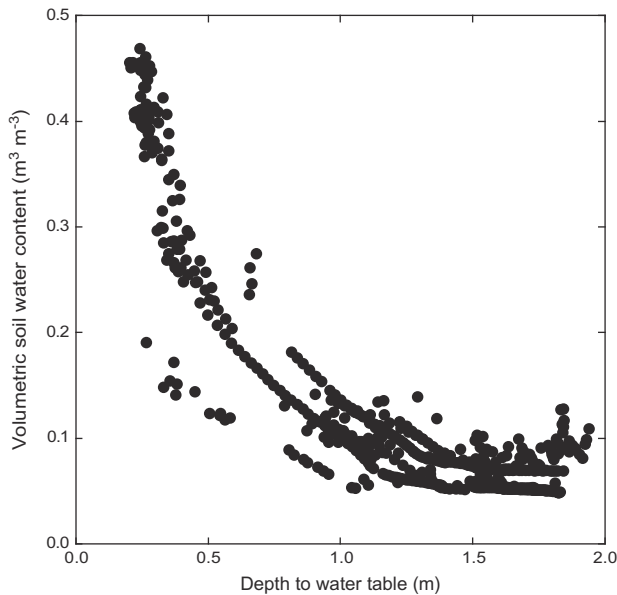


Fig. 2. Relationship between depth to water table and volumetric soil water content in the upper 1 m soil depth monitored from January 2009 to May 2011.

2009 and 2010; >3 kPa). LAI was constant throughout the year, with high values recorded for acacia and Popel, and low values for Tbeng and eucalyptus.

3.2. Transpiration characteristics

In each species, F_d was low in September and October 2009 and high late in the dry season and early in the rainy season in Popel and eucalyptus (Fig. 3). F_d of these species showed seasonal trends similar to those of E_{eq} and VPD (Fig. 1). For Tbeng, F_d was highly variable among sensors and trees. J_s divided by equilibrium evaporation (J_s/E_{eq}) was low in Popel during the dry season in February 2009 and in late January 2010 (Fig. 4). The sharp decrease in J_s/E_{eq} of Popel in the dry season in 2010 was in contrast to Tbeng and eucalyptus. In February 2009, the duration of the decline in J_s/E_{eq} was shorter than two weeks in Popel and was ended by episodic precipitation. Reduced J_s/E_{eq} values corresponded to the timing of lowered θ_{soil} in 2009 and 2010, but were more clearly related to the increasing depth to water table from January to March 2010 (Fig. 5). Although the decrease was less clear, a linear relationship between depth to water table and J_s/E_{eq} was observed in eucalyptus and Tbeng when the analysis was limited to data recorded during one drought period (20 January to 30 March 2010). During this period, depth to water table reached 1.5 m and continued to increase to 1.7 m until a heavy rainfall event (88 mm day^{-1}).

In eucalyptus, sustained reduction in J_s/E_{eq} was observed in the mid rainy season in 2009 during the water-logged period. During this period, J_s/E_{eq} in eucalyptus and depth to water table were positively correlated ($r^2 = 0.53$), whereas no significant relationship was observed for the other species (Fig. 5). The annual minimum J_s/E_{eq} value was observed during the water-logged period (September–November 2009) in eucalyptus and was 40% of the annual maximum, which occurred in the dry season (January 2010) (Fig. 4).

To identify the factor that controls variation in tree water uptake among trees, the means for tree water uptake during the rainy season (1 August to 31 October 2009) and dry season (1 December to 28 February 2010) were calculated and compared with dbh. Eucalyptus showed higher tree water uptake in the dry season than other species of the same dbh, but no difference was

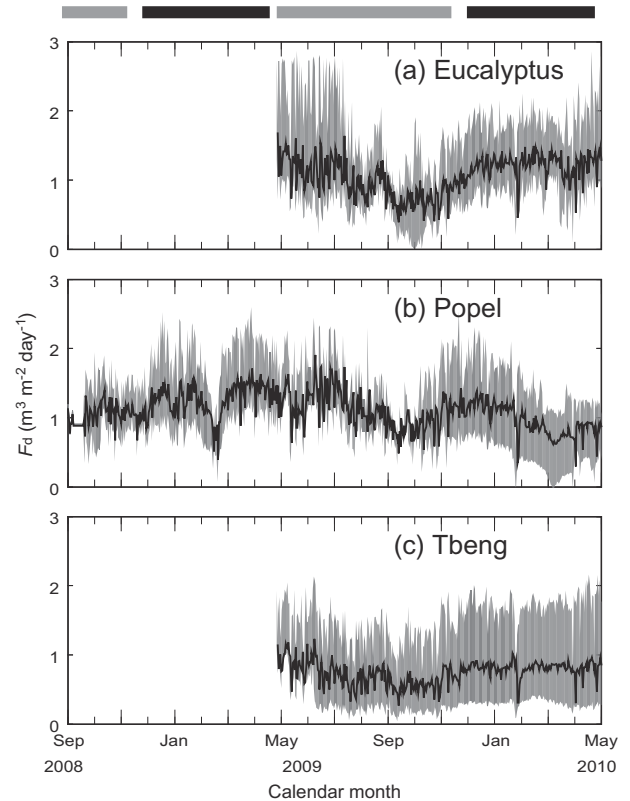


Fig. 3. Seasonal trends in sap flux (F_d) measured by the sensors installed on (a) eucalyptus, (b) Popel and (c) Tbeng. Lines indicate the mean F_d and the gray zones indicate the ranges between the maximum and minimum F_d among individual trees for each species.

observed in the rainy season. Mean tree water uptake was correlated with dbh both in the rainy and dry seasons (Fig. 6). The regression was, however, weaker when the relationship between dbh and tree water uptake was examined among trees within a species. Given the large intra-species variation in mean stem sap flux, tree water uptake differed by a factor of three among trees at each dbh. Among trees in each species, F_d in dry season was strongly correlated with that of the tree in rainy season ($r^2 = 0.88$, 0.99 and 0.96 for eucalyptus, Popel and Tbeng, respectively), which indicated that F_d of the trees changed similarly in response to the changing environment.

4. Discussion

Rising groundwater table depth in the rainy season was partly attributable to the high rainfall relative to E_{eq} , especially in the rainy season. Suzuki et al. (2006) showed that the ratio of annual rainfall to E_{eq} (wetness index) was higher than 1 in many tropical rainy regions, as observed at the present study site (1.35 in 2008).

Previous studies have shown that tree size (sapwood area or dbh) has a strong effect on tree water uptake (Cienciala et al., 2000; Meinzer et al., 2005; McJannet et al., 2007; Kumagai et al., 2008; Jung et al., 2011). At the present study site, a relationship between dbh and tree water uptake was observed among all individual trees, but was less clear within Popel and Tbeng partly because of the large variation in sap flux and narrow range of dbh among trees (Fig. 6). In similarly young reforested areas (20 years old), Dierick and Holscher (2009) also observed inter-species variation in sap flux owing to the narrow range in dbh compared with old-growth forests. Intra-species variation in sap flux may be caused by the tree-level acclimation in transpiration characteristics to

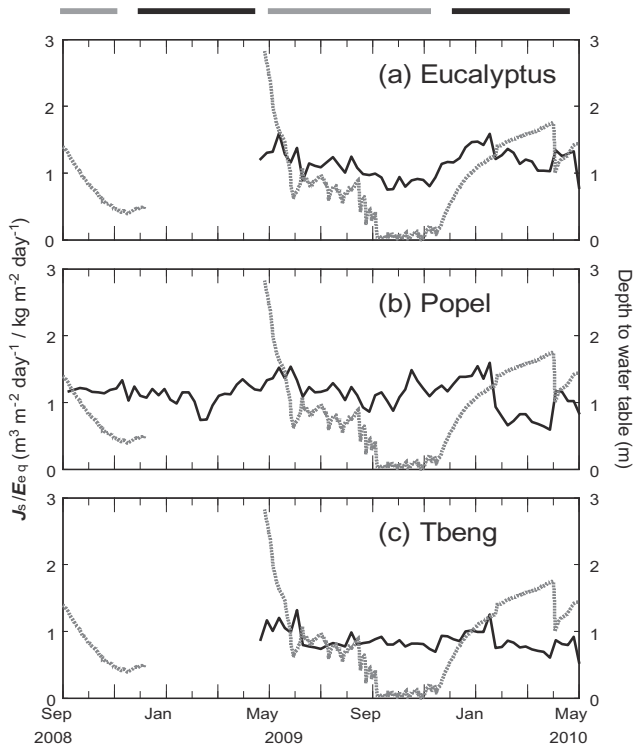


Fig. 4. Seasonal trends in the weekly averages of the ratio of sap flux weighted by the sapwood area of the measured trees (J_s) to equilibrium evaporation (E_{eq}) of (a) eucalyptus, (b) Popel and (c) Tbeng. Dotted lines indicate the depth to water table in each period. Black bars at the top of the figure indicate the rainy seasons, gray bars indicate the dry seasons.

the heterogeneous microenvironments within the small plot (edaphic conditions and soil water conditions) (Granier et al., 2000), especially in *E. camaldulensis*, which is known to show strong intra-species variation (Yunusa et al., 2010). The large variation in sap flux may be the result of different light environments encountered by trees of the same dbh (Granier et al., 1996; McJannet et al., 2007). Highly heterogeneous light environments are indicated by the structure of our study site; some trees are located in small clumps, whereas others are sparsely distributed. Such heterogeneous forest structure is typical in central Cambodia where people have easy access to the forests and patchily harvest trees for daily uses, such as firewood (Top et al., 2004).

The seasonal trends in J_s/E_{eq} were specific to the environments around the present study site and to the occurring species, and were characterized by a decrease in J_s/E_{eq} in the dry season in Popel, a decrease during the water-logged period in eucalyptus, and no clear seasonal trends in Tbeng. Decrease in J_s/E_{eq} under an increasing depth to water table suggested that Popel trees had difficulty meeting the atmospheric evaporative demand (VPD and E_{eq} , Fig. 1) and in accessing the deep groundwater table during the dry season, as observed in species in other forests on the Indochina Peninsula (Pinker et al., 1980). Despite reduction in J_s/E_{eq} with increasing groundwater table depth during a short drought event (20 January to 30 March 2010), the negative effects of the low groundwater table on J_s/E_{eq} were not as severe on the co-existing eucalyptus and Tbeng, which indicates that transpiration characteristics reflect species-specific ecophysiological traits, such as a deeper rooting systems (Eamus et al., 2001; O'Grady et al., 2006, 2009). Species-specific responses to increasing depth to water table suggest that interannual variation in the intensity and duration of the dry season has different influences on transpiration, and possibly on CO_2 exchange, among the species growing at our study

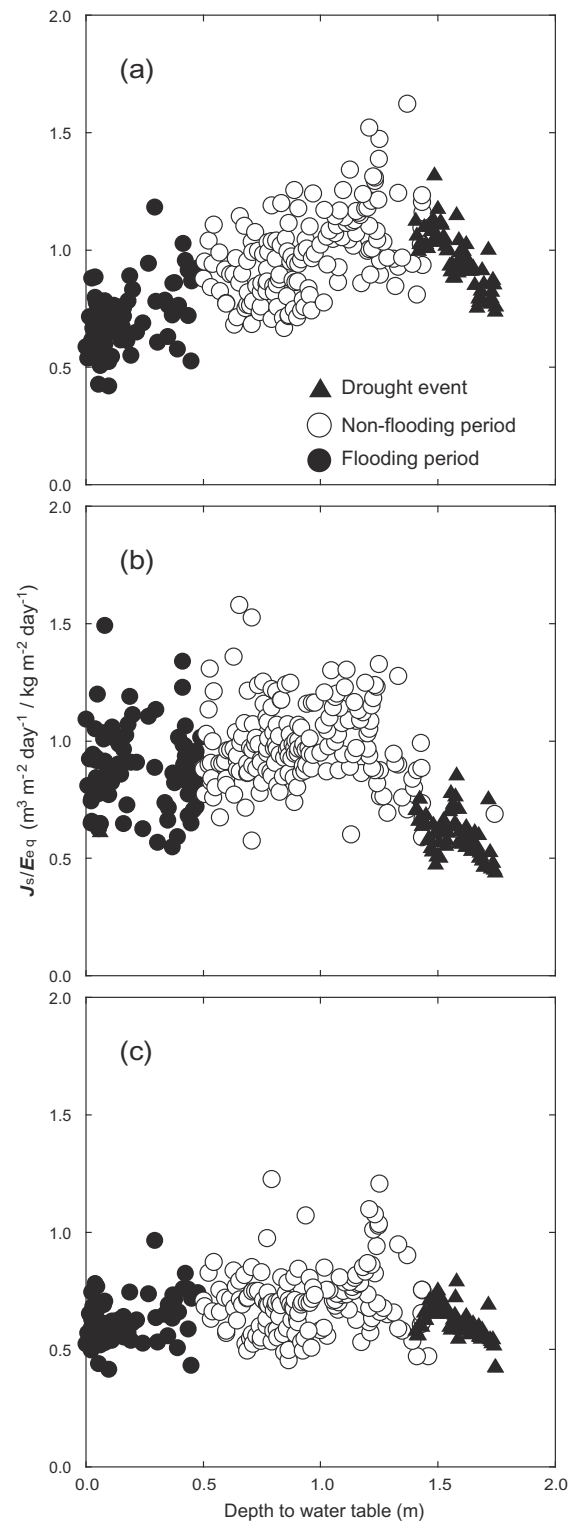


Fig. 5. Relationship between J_s/E_{eq} and the depth to water table for (a) eucalyptus, (b) Popel and (c) Tbeng. Data recorded during a drought event (22 January to 27 March 2009, when episodic rain occurred) are represented by triangles.

site. Interestingly, our recent work (Y. Miyazawa and T. Kumagai, unpublished data) found that eucalyptus showed the lowering of midday leaf water potential to as low levels as the minimum levels in saline regions (Thorburn et al., 1993) and sustained sap flux after sunset. These symptoms are observed in trees under drought conditions in dry seasons (Phillips et al., 1996; David et al., 1997;

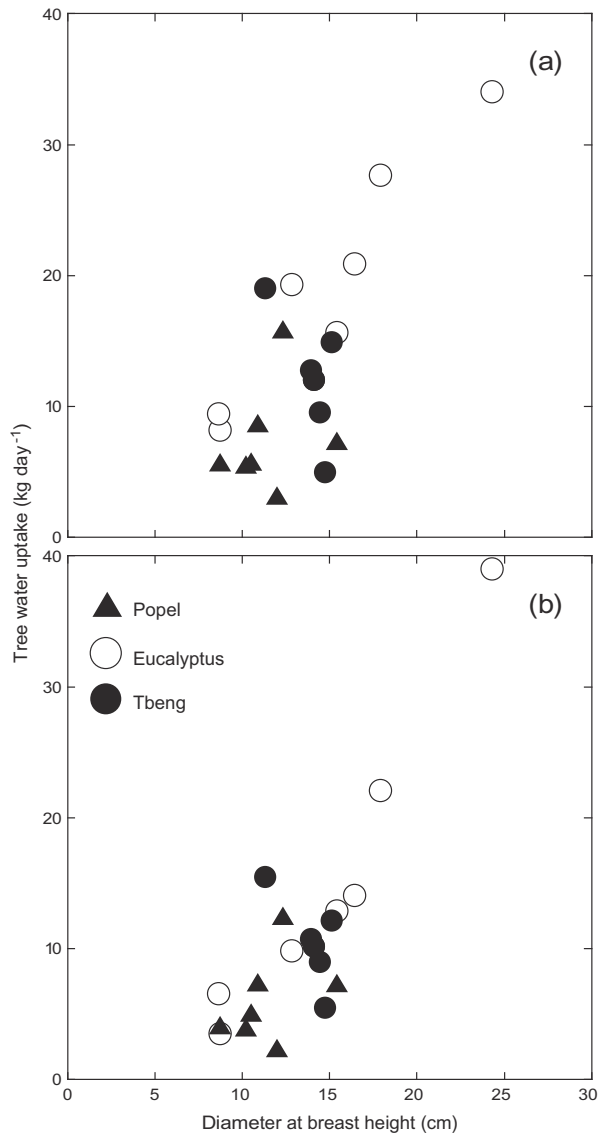


Fig. 6. Diameter at breast height and mean tree water uptake by an individual tree during (a) the mid dry season (1 January to 28 February 2010) and (b) the mid rainy season (1 August to 31 October 2009).

Pfautsch et al., 2011). These results suggested that eucalyptus maintained the transpiration rate at a high level under drought conditions and did not control stomata to maintain leaf water potential at a high level (Teskey et al., 1983; Hubbard et al., 2001; Delzon et al., 2004). Such symptoms were, however, not observed in T beng or Popel in response to drought.

Although lowered J_s/E_{eq} with increasing depth to water table was detected, the degree and duration of reduction of J_s/E_{eq} in the present study were modest compared with previous studies that reported reduced transpiration under drought conditions (Pereira et al., 1987; Roberts et al., 1993; Goulden, 1996; Harris et al., 2004; Kume et al., 2007; McJannet et al., 2007; O'Grady et al., 2008). In Popel, which showed the most pronounced decline in J_s/E_{eq} , J_s/E_{eq} decreased only by 30–50% of the annual mean. LAI (Fig. 1e) and leaf-level gas exchange measurements (Y. Miyazawa and T. Kumagai, unpublished data) did not show clear changes in the dry season as a result of soil drought. This is partly because of the relatively shallow groundwater table even in the middle of the dry season (1.8 m below the soil surface), which was lower than that observed in previous studies that reported tree access

to the groundwater in other regions (Dye, 1996; Cleverly et al., 2006; O'Grady et al., 2009) and at a different study site in the Indochina Peninsula (Tanaka et al., 2004). Because our research was carried out within a short period, we did not encounter an episodic severe drought or greatly reduced groundwater level during the measurement period. Further studies are necessary to identify how frequently severe and mild droughts occur in the study region and to reveal the effects of more severe drought.

Tanaka et al. (2003) observed a higher transpiration rate in the dry season in montane evergreen forest and attributed the high transpiration rate to the high atmospheric evaporative demand and access to sufficient water from the deep soil (Tanaka et al., 2004). In the present study, lower J_s values in the rainy season than in the dry season in eucalyptus were not a result of reduced E_{eq} , but rather of decreased J_s/E_{eq} because of the shallow groundwater table (Fig. 4) (Granier et al., 1990, but see Oren et al., 1999, 2001). The absence of reduced J_s/E_{eq} in the native species (T beng and Popel) suggested that this non-endemic eucalyptus species (river gum) could not physiologically adapt to the environment in the present study site, although the species experiences frequent flooding in its native riparian habitat (Thorburn et al., 1993; Dawson and Pate, 1996; Thomas et al., 1999). In eucalyptus J_s/E_{eq} decreased during the water-logged period, possibly owing to the detrimental effects on root water uptake of anoxic conditions in the rhizosphere (Naumburg et al., 2005). However, J_s/E_{eq} decreased without reduced LAI (Fig. 1e) in contrast to a previous study (Santiago et al., 2000). Further, our recent research (Y. Miyazawa and T. Kumagai, unpublished data) found decreased J_s/E_{eq} without coincident changes in leaf traits, although reduction in leaf gas exchange rates in relation to transpiration has been reported for other species under flooding (Blanke and Cooke, 2004; Yetisir et al., 2006; Aroca et al., 2012), indicating that other factors are responsible for the decreased J_s/E_{eq} , such as the restriction of maximum root water uptake to low levels and lowered J_s in evaporative midday conditions without clear influences on leaf-level ecophysiological traits. Because large variation in the duration of flooding is expected among years, similar to variation in the intensity and duration of drought in the present study region (Fig. 1a), flooding would be a driving factor for the interannual variation in J_s/E_{eq} in eucalyptus.

It should be noted that we calculated R_n using a simple equation derived from data obtained at a different study site and uncertainty in the estimated R_n might have influenced the results presented in Figs. 4 and 5. An alternative estimate of R_n based on estimated albedo of 0.16–0.19, which approximated albedo during the low LAI period in a deciduous rubber plantation, and estimates of upward and downward longwave radiation (Brutsaert, 1975; Leuning et al., 1995) were independently obtained and were positively correlated with R_n used in this study (slope = 0.993–1.118). Although albedo can drastically change before leaf fall and after the new leaf flush (February–April at the present study site), albedo remains relatively stable between leaf appearance (Moore et al., 1996; Schmid et al., 2000). On the assumption that albedo did not change seasonally under the constant LAI (Fig. 1e), bias in R_n may change absolute values of E_{eq} , but would not affect the response of J_s/E_{eq} to depth to water table and its inter-species variation (Figs. 4 and 5). Therefore, during the period without such leaf phenological events, including the periods when species-specific changes in J_s/E_{eq} were observed, the assumption of constant albedo would not alter the findings of this study.

In conclusion, the three species investigated showed transpiration characteristics that were closely related to the groundwater table depth. Given that the seasonal pattern of depth to water table was decoupled from the onset of the dry and rainy seasons defined by the rainfall distribution, the transpiration characteristics of the forest were governed more by the groundwater dynamics and less

by the onset of the rainy or dry season, which illustrated the importance of *in situ* monitoring of tree sap flux and obtaining information on groundwater dynamics.

Given the inter-species variation in transpiration characteristics under seasonally and interannually dynamic depth to water table, our work implies that changes in species composition of forests in the central Cambodian plains will alter the transpiration characteristics of the forests, not only quantitatively but also qualitatively (Pataki and Oren, 2003; Delzon and Loustau, 2005; Herbst et al., 2008). Prolonged flooding would reduce transpiration in eucalyptus-dominated forest but to a lesser extent in Popel- or Tbeg-dominated forests. Evaluation of forest transpiration in this region requires detailed information on the soil water environments, transpiration characteristics of the component species, and the differences in species composition.

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References

- Aroca, R., Porcel, R., Ruiz-Lozano, J.M., 2012. Regulation of root water uptake under abiotic stress conditions. *J. Exp. Bot.* 63, 43–57.
- Blanke, M.M., Cooke, D.T., 2004. Effects of flooding and drought on stomatal activity, transpiration, photosynthesis, water potential and water channel activity in strawberry stolons and leaves. *Plant Growth Regul.* 42, 153–160.
- Bruijnzeel, L.A., 2004. Hydrological functions of tropical forests: not seeing the soil for the trees? *Agr. Ecosyst. Environ.* 104, 185–228.
- Brutsaert, W., 1975. Derivable formula for long-wave radiation from clear skies. *Water Resour. Res.* 11, 742–744.
- Calder, I.R., Hall, R.L., Prasanna, K.T., 1993. Hydrological impact of eucalyptus plantation in India. *J. Hydrol.* 150, 635–648.
- Cienciala, E., Kucera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. *J. Hydrol.* 236, 109–120.
- Cleverly, J.R., Dahm, C.N., Thibault, J.R., McDonnell, D.E., Coonrod, J.E.A., 2006. Riparian ecohydrology: regulation of water flux from the ground to the atmosphere in the middle Rio Grande, New Mexico. *Hydrol. Process.* 20, 3207–3225.
- David, T.S., Ferreira, M.L., David, J.S., Pereira, J.S., 1997. Transpiration from a mature *Eucalyptus globulus* plantation in Portugal during a spring-summer period of progressively higher water deficit. *Oecologia* 110, 153–159.
- Dawson, T.E., Pate, J.S., 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* 107, 13–20.
- Delzon, S., Loustau, D., 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agric. For. Meteorol.* 129, 105–119.
- Delzon, S., Sartore, M., Burret, R., Dewar, R., Loustau, D., 2004. Hydraulic responses to height growth in maritime pine trees. *Plant Cell Environ.* 27, 1077–1087.
- Dierick, D., Holscher, D., 2009. Species-specific tree water use characteristics in reforestation stands in the Philippines. *Agric. For. Meteorol.* 149, 1317–1326.
- Dye, P.J., 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiol.* 16, 233–238.
- Eamus, D., O'Grady, A.P., Hutley, L., 2000. Dry season conditions determine wet season water use in the wet-dry tropical savannas of northern Australia. *Tree Physiol.* 20, 1219–1226.
- Eamus, D., Hutley, L.B., O'Grady, A.P., 2001. Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiol.* 21, 977–988.
- Fisher, R.A., Williams, M., Do Vale, R.L., Da Costa, A.L., Meir, P., 2006. Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant Cell Environ.* 29, 151–165.
- Franco, A.C., 1998. Seasonal patterns of gas exchange, water relations and growth of *roupala montana*, an evergreen savanna species. *Plant Ecol.* 136, 69–76.
- Goulden, M.L., 1996. Carbon assimilation and water-use efficiency by neighboring Mediterranean-climate oaks that differ in water access. *Tree Physiol.* 16, 417–424.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3, 309–319.
- Granier, A., Bobay, V., Gash, J.H.C., Gelpe, J., Saugier, B., Shuttleworth, W.J., 1990. Vapor flux-density and transpiration rate comparisons in a stand of Maritime pine (*Pinus-pinaster* ait) in Les-Landes forest. *Agric. For. Meteorol.* 51, 309–319.
- Granier, A., Huc, R., Barigah, S.T., 1996. Transpiration of natural rain forest and its dependence on climatic factors. *Agric. For. Meteorol.* 78, 19–29.
- Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. *Agric. For. Meteorol.* 100, 291–308.
- Harris, P.P., Huntingford, C., Cox, P.M., Gash, J.H.C., Malhi, Y., 2004. Effect of soil moisture on canopy conductance of Amazonian rainforest. *Agric. For. Meteorol.* 122, 215–227.
- Herbst, M., Rosier, P.T.W., Morecroft, M.D., Gowing, D.J., 2008. Comparative measurements of transpiration and canopy conductance in two mixed deciduous woodlands differing in structure and species composition. *Tree Physiol.* 28, 959–970.
- Hornbeck, J.W., Adams, M.B., Corbett, E.S., Verry, E.S., Lynch, J.A., 1993. Long-term impacts of forest treatments on water yield – a summary for northeastern USA. *J. Hydrol.* 150, 323–344.
- Hubbard, R.M., Ryan, M.G., Stiller, V., Sperry, J.S., 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell Environ.* 24, 113–121.
- Hutley, L.B., O'Grady, A.P., Eamus, D., 2000. Evapotranspiration from eucalypt open-forest savanna of northern Australia. *Funct. Ecol.* 14, 183–194.
- Jones, H.G., 1992. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*, second ed. Cambridge University Press, New York, USA.
- Jung, E.Y., Otieno, D., Lee, B., Lim, J.H., Kang, S.K., Schmidt, M.W.T., Tenhunen, J., 2011. Up-scaling to stand transpiration of an Asian temperate mixed-deciduous forest from single tree sapflow measurements. *Plant Ecol.* 212, 383–395.
- Kelliher, F.M., Leuning, R., Raupach, M.R., Schulze, E.D., 1995. Maximum conductances for evaporation from global vegetation types. *Agric. For. Meteorol.* 73, 1–16.
- Kumagai, T., Aoki, S., Shimizu, T., Otsuki, K., 2007. Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiol.* 27, 161–168.
- Kumagai, T., Tateishi, M., Shimizu, T., Otsuki, K., 2008. Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed. *Agric. For. Meteorol.* 148, 1444–1455.
- Kume, T., Takizawa, H., Yoshifuji, N., Tanaka, K., Tantasirin, C., Tanaka, N., Suzuki, M., 2007. Impact of soil drought on sap flow and water status of evergreen trees in a tropical monsoon forest in northern Thailand. *Forest Ecol. Manage.* 238, 220–230.
- Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Frachebourg, J.M., Hultman, N., 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiol.* 21, 299–308.
- Leuning, R., Cleugh, H.A., Zegelin, S.J., Hughes, D., 2005. Carbon and water fluxes over a temperate eucalyptus forest and a tropical wet/dry savanna in Australia: measurements and comparison with MODIS remote sensing estimates. *Agric. For. Meteorol.* 129, 151–173.
- Leuning, R., Kelliher, F.M., de Pury, D.G.G., Schulze, E.D., 1995. Leaf nitrogen, photosynthesis, conductance and transpiration – scaling from leaves to canopies. *Plant Cell Environ.* 18, 1183–1200.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- McJannet, D., Fitch, P., Disher, M., Wallace, J., 2007. Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. *Hydrol. Process.* 21, 3549–3564.
- McNaughton, K.G., Jarvis, P.G., 1991. Effects of spatial scale on stomatal control of transpiration. *Agric. For. Meteorol.* 54, 279–302.
- Meinzer, F.C., Goldstein, G., Franco, A.C., Bustamante, M., Igler, E., Jackson, P., Caldas, L., Rundel, P.W., 1999. Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. *Funct. Ecol.* 13, 273–282.
- Meinzer, F.C., Bond, B.J., Warren, J.M., Woodruff, D.R., 2005. Does water transport scale universally with tree size? *Funct. Ecol.* 19, 558–565.
- Mielke, M.S., Oliva, M.A., de Barros, N.F., Penchel, R.M., Martinez, C.A., da Fonseca, S., de Almeida, A.C., 2000. Leaf gas exchange in a clonal eucalypt plantation as related to soil moisture, leaf water potential and microclimate variables. *Trees-Struct. Funct.* 14, 263–270.

- Moore, K.E., Fitzjarrald, D.R., Sakai, R.K., Goulden, M.L., Munger, J.W., Wofsy, S.C., 1996. Seasonal variation in radiative and turbulent exchange at a deciduous forest in central Massachusetts. *J. Appl. Meteorol.* 35, 122–134.
- Naumburg, E., Mata-Gonzalez, R., Hunter, R.G., McLendon, T., Martin, D.W., 2005. Phreatophytic vegetation and groundwater fluctuations: a review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environ. Manage.* 35, 726–740.
- O'Grady, A.P., Eamus, D., Cook, P.G., Lamontagne, S., 2006. Comparative water use by the riparian trees *Melaleuca argentea* and *Corymbia bella* in the wet-dry tropics of northern Australia. *Tree Physiol.* 26, 219–228.
- O'Grady, A.P., Worledge, D., Battaglia, M., 2008. Constraints on transpiration of eucalyptus globulus in southern Tasmania, Australia. *Agric. Forest Meteorol.* 148, 453–465.
- O'Grady, A.P., Cook, P.G., Eamus, D., Duguid, A., Wischusen, J.D.H., Fass, T., Worledge, D., 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia* 160, 643–655.
- Oren, R., Phillips, N., Ewers, B.E., Pataki, D.E., Megonigal, J.P., 1999. Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree Physiol.* 19, 337–347.
- Oren, R., Sperry, J.S., Ewers, B.E., Pataki, D.E., Phillips, N., Megonigal, J.P., 2001. Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded *Taxodium distichum* I. Forest: Hydraulic and non-hydraulic effects. *Oecologia* 126, 21–29.
- Pataki, D.E., Oren, R., 2003. Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest. *Adv. Water Resour.* 26, 1267–1278.
- Penman, H.L., 1948. Natural evaporation from open water, bare soil and grass. *Proc. Roy. Soc. London A* 193, 120–145.
- Pereira, J.S., Tenhunen, J.D., Lange, O.L., 1987. Stomatal control of photosynthesis of *Eucalyptus globulus* labill - trees under field conditions in Portugal. *J. Exp. Bot.* 38, 1678–1688.
- Pfautsch, S., Keitel, C., Turnbull, T.L., Braimbridge, M.J., Wright, T.E., Simpson, R.R., O'Brien, J.A., Adams, M.A., 2011. Diurnal patterns of water use in *Eucalyptus victrix* indicate pronounced desiccation-rehydration cycles despite unlimited water supply. *Tree Physiol.* 31, 1041–1051.
- Phillips, N., Oren, R., Zimmermann, R., 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant Cell Environ.* 19, 983–990.
- Pinker, R.T., Thompson, O.E., Eck, T.F., 1980. The energy-balance of a tropical evergreen forest. *J. Appl. Meteorol.* 19, 1341–1350.
- Priestley, C.H.B., Taylor, R.J., 1972. Assessment of surface heat-flux and evaporation using large-scale parameters. *Mon. Weather Rev.* 100, 81–92.
- Prior, L.D., Bowman, D., Eamus, D., 2004. Seasonal differences in leaf attributes in Australian tropical tree species: family and habitat comparisons. *Funct. Ecol.* 18, 707–718.
- Roberts, J., Cabral, O.M.R., Fisch, G., Molion, L.C.B., Moore, C.J., Shuttleworth, W.J., 1993. Transpiration from an Amazonian rain-forest calculated from stomatal conductance measurements. *Agric. For. Meteorol.* 65, 175–196.
- Santiago, L.S., Goldstein, G., Meinzer, F.C., Fownes, J.H., Mueller-Dombois, D., 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiol.* 20, 673–681.
- Schmid, H.P., Grimmond, C.S.B., Cropley, F., Offerle, B., Su, H.B., 2000. Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agric. For. Meteorol.* 103, 357–374.
- SCW, 2006. Atlas of Cambodia: national poverty and environment maps. Save Cambodia's Wildlife, Phnom Penh, Cambodia.
- Suzuki, R., Xu, J.Q., Motoya, K., 2006. Global analyses of satellite-derived vegetation index related to climatological wetness and warmth. *Int. J. Climatol.* 26, 425–438.
- Tanaka, K., Takizawa, H., Tanaka, N., Kosaka, I., Yoshifuji, N., Tantasirin, C., Piman, S., Suzuki, M., Tangtham, N., 2003. Transpiration peak over a hill evergreen forest in northern Thailand in the late dry season: assessing the seasonal changes in evapotranspiration using a multilayer model. *J. Geophys. Res.* 108, 4533.
- Tanaka, K., Takizawa, H., Kume, T., Xu, J.Q., Tantasirin, C., Suzuki, M., 2004. Impact of rooting depth and soil hydraulic properties on the transpiration peak of an evergreen forest in northern Thailand in the late dry season. *J. Geophys. Res.-Atmos.* 109.
- Tanaka, N., Kume, T., Yoshifuji, N., Tanaka, K., Takizawa, H., Shiraki, K., Tantasirin, C., Tangtham, N., Suzuki, M., 2008. A review of evapotranspiration estimates from tropical forests in Thailand and adjacent regions. *Agric. For. Meteorol.* 148, 807–819.
- Teskey, R.O., Sheriff, D.W., 1996. Water use by *Pinus radiata* trees in a plantation. *Tree Physiol.* 16, 273–279.
- Teskey, R.O., Hinckley, T.M., Grier, C.C., 1983. Effect of interruption of flow path on stomatal conductance of *Abies-amabilis*. *J. Exp. Bot.* 34, 1251–1259.
- Thomas, D.S., Eamus, D., Bell, D., 1999. Optimization theory of stomatal behaviour – II. Stomatal responses of several tree species of north Australia to changes in light, soil and atmospheric water content and temperature. *J. Exp. Bot.* 50, 393–400.
- Thorburn, P.J., Hatton, T.J., Walker, G.R., 1993. Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. *J. Hydrol.* 150, 563–587.
- Top, N., Mizoue, N., Ito, S., Kai, S., 2004. Spatial analysis of woodfuel supply and demand in Kampong Thom Province, Cambodia. *Forest Ecol. Manage.* 194, 369–378.
- Tsuruta, K., Kume, T., Komatsu, H., Higashi, N., Umabayashi, T., Kumagai, T.o., Otsuki, K., 2010. Azimuthal variations of sap flux density within Japanese cypress xylem trunks and their effects on tree transpiration estimates. *J. Forest Res.* 15, 398–403.
- Whitehead, D., Beadle, C.L., 2004. Physiological regulation of productivity and water use in eucalyptus: a review. *Forest Ecol. Manage.* 193, 113–140.
- Williams, L.J., Bunyavejchewin, S., Baker, P.J., 2008. Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. *Oecologia* 155, 571–582.
- Yetsir, H., Caliskan, M.E., Soylu, S., Sakar, M., 2006. Some physiological and growth responses of watermelon *Citrullus lanatus* (Thunb.) Matsum. and Nakai grafted onto *Lagenaria siceraria* to flooding. *Environ. Exp. Bot.* 58, 1–8.
- Yunusa, I.A.M., Aumann, C.D., Rab, M.A., Merrick, N., Fisher, P.D., Eberbach, P.L., Eamus, D., 2010. Topographical and seasonal trends in transpiration by two co-occurring *Eucalyptus* species during two contrasting years in a low rainfall environment. *Agric. Forest Meteorol.* 150, 1234–1244.
- Zeppel, M.J.B., Murray, B.R., Barton, C., Eamus, D., 2004. Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. *Funct. Plant Biol.* 31, 461–470.