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Dry-season water utilization by trees growing on thin karst soils in a seasonal tropical rainforest of Xishuangbanna, Southwest China

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ABSTRACT

Stable isotopes were used to evaluate water utilization for three tree species (*Cleistanthus sumatranus*, *Lasiococca comberi* var. *pseudoverticillata* and *Celtis wightii*) growing on karst soils in the seasonal tropical rainforest of Xishuangbanna, Southwest China. The soil on the site is only 40 cm thick but was underlain by thick limestone bedrock with large water storage capacity. Dense radiational fog occurred frequently during the pronounced dry season. Isotope composition of water in xylem, soil and fog were analysed, and soil and stem porous water content were measured concurrently to determine the proportion of water deriving from fog, soil and bedrock by adult trees and seedlings at the peak of the dry season. Results indicated that *C. wightii* seedlings suffered stronger water stress and greatly relied on available moisture from fog (23.8% on average). This suggests that fog water was an important source for seedling growth during the pronounced dry season. In contrast, adult trees had little or negligible water uptake from fog moisture (3–7% on average) but derived around 63–85% of their water from bedrock sources. Water held within bedrock was essential for meeting plant transpiration requirements over the dry season drought. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS fog water; limestone ecosystem; stable isotopes; water utilization

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INTRODUCTION

Many species-rich tropical forests experience a prolonged dry season during which little or no rain falls and upper soil layers undergo severe drying (Jackson *et al*., 1995; Querejeta *et al*., 2007). Therefore, the distribution and accessibility of soil water greatly influence plant growth and survival (Drake and Franks, 2003; Andrade *et al*., 2005; West *et al*., 2007). A variety of traits allow plants to persist under prolonged dry conditions, such as early flowering, leaf and stem succulence and deep roots that access permanent water sources (Corbin *et al*., 2005; Goldstein *et al*., 2008). It also has been suggested that competition for limited water source may be minimized, and therefore, species diversity maximized, by intensive spatial and temporal partitioning of resource utilization (Meinzer *et al*., 1999; Bonal *et al*., 2000; Borchert *et al*., 2004; Schwinning, 2008). For plants growing together in natural communities, differential use of water resources has been shown across different growth forms (Ehleringer *et al*., 1991; Canadell *et al*., 1996; Jackson *et al*., 1999; Goldstein *et al*., 2008) and within similar growth forms (Pate and Dawson, 1999; Stratton *et al*., 2000; Querejeta *et al*., 2006). However, it is difficult to draw inferences about spatial partitioning of soil water in tropical forests on the basis of direct observation of rooting patterns because of the large and intricate root biomass, high species diversity characteristic of these ecosystems, the uncertain relationship between the presence of roots in a particular soil layer and the magnitude of their contribution to the water budget of a plant (Jackson *et al*., 1995; Moreira *et al*., 1997, 2000; Chapotin *et al*., 2006). The stable isotope technique has greatly facilitated the identification and separation of different water sources (rain, fog water, soil water etc.) that might be used by plants by comparing the isotope composition of xylem water with that of potential water sources (Sternberg and Swart, 1987; Ehleringer *et al*., 1991; Lin *et al*., 1996; Dawson *et al*., 2002; Nippert and Knapp, 2007).

Limestone ecosystem is one of the principal vegetation types in tropical Yunnan of southwest China. Because of

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the great diversity of habitat and topography, limestone ecosystem is extremely diverse in community types and very rich in endemic taxa in this area. Within the seasonal tropical rainforest (locally termed as limestone tropical seasonal moist forest; Zhu *et al.*, 1998), most plants remain evergreen and continue to transpire during the 4–6 month dry season when rain is sparse. This indicates that shallow soil does not represent a major hindrance for the establishment and growth of tree species in the forest. During the dry season drought, thin soils often lack sufficient water-holding capacity to support plant growth, and trees may depend on water stored within the thick zones of limestone bedrock (Li *et al.*, 1996). Tree roots have been observed metres deep into bedrock along joint traces and fissures in this seasonal dry ecosystems (Zhu *et al.*, 1998), suggesting that not only the soil but also the bedrock itself may serve an important ecosystem function. In addition, dense radiation fog occurs frequently within the forest site during the pronounced dry season (Figure 1(a)). This means fog may be of particular ecological significance for the ecosystem, as the period of most frequent fog inundations coincide with the dry season drought. Although it is reasonable to expect that plants in this seasonal tropical rainforest might rely on water stored in the bedrock and water from radiational fog (Zhu *et al.*, 1998), no work had been done to test if this was true.

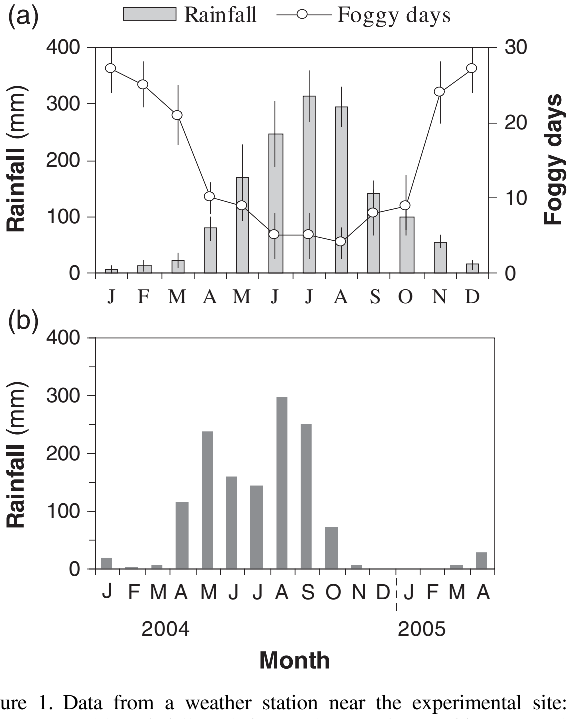

Figure 1. Data from a weather station near the experimental site: (a) average monthly rainfall and foggy days during 1965–2003 and (b) monthly rainfall distribution and air temperature over the dry season of 2004–2005. Vertical arrow indicates sampling date for plant and soil samples. Vertical crossed bar represents ± 1 standard error.

The objective of this study was to determine the dry-season water utilization for three important evergreen tree species, *Cleistanthus sumatranus*, *Lasiococca comberi* var. *pseudoverticillata* and *Celtis wightii*, in a seasonal tropical rainforest of Xishuangbanna, by sampling the stable isotope ratios (δD and δ^{18}O) of water in soil/bedrock, fog and non-photosynthetic tissue. Gravimetric soil water content (SWC) and stem water content were also measured during dry seasons. Specifically, we tested the use of fog water by adult trees and seedlings. We hypothesized that (i) adult trees utilize water primarily from greater depths in the bedrock profile and are experiencing less water stress; (ii) tree seedlings, whose roots are limited to the uppermost soil layer, would experience more severe water stress and (iii) seedlings may rely on water supplies from radiational fog during dry seasons.

MATERIALS AND METHODS

Site description

The study was conducted at a seasonal tropical rainforest site located on a small karst hill in Xishuangbanna, Southwest China (21°55′39″N, 101°15′55″E, 700 m a.s.l.). The dominant plant species are *L. comberi* var. *pseudoverticillata* and *C. sumatranus*. This type of evergreen forest is primarily formed on upper slopes, shady slopes or tops of lower hills with more than 80% of rock outcrops between altitudes 650–800 m (Zhu *et al.*, 1998). There are two distinctive tree layers, with the upper layer 23 m tall on average and the lower layer 5–16 m tall. Some deciduous emergent trees, such as *Tetrameles nudiflora*, *Garuga pinnata* and *Chukrasia tabularis*, are sparsely dotted through the forest. In this forest, woody climbers are very abundant, and vascular epiphytes with small leaves are frequent. This forest shows an intense tropical tendency in forest flora and is closely related to Malaysian forests in flora. Slope of the study hill is about 13° and its aspect is northwest. Soil is very shallow, discontinuous and rocky and is classified as Lithic Leptosol. Organic matter content of the shallow soil is around 6.2% (Li *et al.*, 1996). Depth of the water table is estimated to be at least below 10 m (Li, 2008). More detailed information about the site is provided by Zhu *et al.* (1998).

This region has a strongly seasonal climate with two main air masses alternating during the year. Between May and October (rainy season), the southwest monsoon from the Indian Ocean delivers 80–90% of the annual rainfall without influence from the Pacific typhoons, whereas the southern edges of the subtropical jet streams dominate the climate between November and April (dry season). The dry season includes a foggy sub-season from November to February, which is characterized by highest frequency of radiation fogs during the night and the morning, and a hot sub-season from March to April, which is characterized by dry and hot weather during the afternoon and with dense radiation fogs during the morning only (Figure 1(a)). Thus, radiation fogs occur nearly every day from November to April and are heaviest from midnight (23:00–02:00) until mid-morning (09:00–11:00) when the daily temperature difference is greatest. This area has fog about 37% of the time during the dry season period, with a maximum of 46% during foggy sub-season (Liu *et al*., 2004).

Long-term climate records (1965–2003) as measured at a nearby weather station southeast from the study site showed that the mean annual air temperature is 21.7 °C with a maximum monthly temperature of 25.7 °C for the hottest month (June) and a monthly minimum of 15.9 °C for the coldest month (January). Temperatures exceeding 38 °C often occur during March and April (peak of the dry season) and are always associated with a low relative humidity (less than 40%). The mean annual rainfall is 1454 mm, of which 87% occurs in the rainy season versus 13% in the pronounced 6-month dry season (Figure 1(a)). Class A pan annual evaporation varies between 1000 and 1200 mm. The mean monthly relative humidity is 87%. The mean annual wind speed is $0.7\,\mathrm{m\,s^{-1}}$, and the frequency of calm days is about 75% (Liu *et al*., 2004).

Water, vegetation and soil sampling

Water samples for isotope analysis were collected from fog drip, xylem water and soil/bedrock water. Six v-shape troughs (0.3 × 2.0 m), each connected with a plastic bottle, were mounted 0.7 m above the forest floor and were placed in a random pattern to collect fog dripping from the canopy. To reduce the number of samples for isotope analysis, a volume of water proportional to the volume collected by each collector for each sampling event was combined after collection. Fog drip sampling was performed weekly at or near the peak of a fog drip event but before isotopic fractionation had occurred from re-evaporation (Dawson, 1998). Daily fog drip amounts were measured from November 2004 to April 2005. Fog water samples were stored in sealed screw-cap borosilicate glass vials, wrapped in Parafilm (American National Can company, Chincago IL, USA) and frozen (−20 °C) until later analysis.

Plants were sampled at the early (2 November 2004) and the peak (5 March 2005) dry season over the 2005 dry season. On both occasions (at midday), xylem samples were obtained from each of the three selected adult trees for *C. sumatranus*, *L. comberi* var. *pseudoverticillata* and *C. wightii*. Xylem samples were obtained either by extracting small cylinders of wood with an increment borer or by cutting suberized mature stem segments from each of the four cardinal directions when possible. Seedling xylem samples were obtained from five randomly selected *C. wightii* seedlings (<2 years old and <15 cm high) that emerged nearby the adult trees. Phloem tissue was removed from plant stem samples (Ehleringer *et al*., 2000), and samples were placed into vials immediately upon collection. For seedlings, basal culm and root tissue just below the soil surface level were harvested, taking care to exclude photosynthetic tissue. This methodology, assuming that evaporative processes have not affected plant water in non-photosynthetic tissue, permits the analysis of water taken up by roots, rather than directly by foliage (Dawson, 1998; Corbin *et al*., 2005). In addition, the stem water content of 3–5 stems from three individuals of each species and from seedlings were measured according to differences in sample weight before and after thorough water extraction (105 °C, 24 h). For stem water content and isotope determinations, the same adult trees were sampled repeatedly on successive dates (November 2004 and March 2005). Whereas for seedlings, sampling in November used most of the available tissue and effectively killed the plants. As a result, subsequent March sampling used different seedlings with similar size and nearby location.

Soil/bedrock samples were collected at the same time of plant sampling at the peak of the dry season. Two soil pits of 1.0 m in diameter were manually excavated. The pits were located within 2 m of the base of a *C. wightii* tree and *C. sumatranus* trees to get a visual inspection of rooting depths as well as root distribution. Soil/bedrock samples were taken from soil pit sidewalls immediately after excavation for SWC measurement and for isotope analysis. The irregular spatial distribution of soil pockets and bedrock strata in the soil/bedrock profiles requires more extensive sampling to obtain a representative estimate of soil water storage capacity. Pits were only dug down to a depth of 1.4 m because of technical limitations, but we did observe that some roots still extended into deeper layers through cracks and crevices in the bedrock. Pit excavation exposed a rocky, shallow soil about 40 cm deep overlying heterogeneous fractured limestone bedrock in which some soil-filled cracks and crevices were encountered. Samples were taken at approximately 5 cm increments in the first 20 cm depth, then every 10 cm interval below the 20 cm depth. For each depth, three replicate soil/bedrock samples were collected about 3 cm deep (horizontally) into the sidewalls of the pits to avoid alteration of water isotopic composition by evaporative enrichment during the process of excavation.

The isotopic composition of plant xylem water was assumed to be an integrated measure of the water in the soil horizons from which the plant actively took up water and was compared with the gradient of isotopic values through the soil profile (Ehleringer *et al*., 2000). SWC was determined from the sample weight loss by drying samples at 105 °C for 24 h. Soil and plant tissue samples were stored as described previously, and were kept in a cooler with ice in the field and maintained frozen (−20 °C) in the laboratory prior to water extraction.

Soil and stem water was extracted from the soil and stem samples by a cryogenic vacuum distillation method (Ehleringer *et al.*, 2000). The extracted waters were sealed in vials and frozen until later analysis. The H and O isotopic composition of all water samples was determined from a gas sample generated from pure liquid introduced into an isotope ratio mass spectrometer (Finnigan MAT252, Thermo Fisher Scientific Inc., Waltham, USA) at the Test Center of Lanzhou Branch, the Chinese Academy of Sciences. Isotope ratios are expressed in ‰ relative to Vienna Standard Mean Ocean Water (δD and δ^{18}O; Ehleringer *et al.*, 1991). The precision (± standard error) of H and O isotope measurements are 1.0‰ and 0.5‰, respectively.

The proportion of water derived from different sources at the peak of the dry season was estimated for each species with the IsoSource mixing model (Phillips and Gregg, 2003). This model gives the proportion of feasible sources when there are a high number of potential sources and is based solely on isotopic mass balance constraints. In this study, the fog water was considered as a distinct water source because before the peak dry season sampling, there was more than 3–4 months without rainfall except fog water input. Hence, three distinct water sources (fog water, soil and bedrock water) were considered and both δ^{18}O and δD data were used for the model calculations. In the calculations, average isotopic value for fog water is the volume-weighted mean value of fog drip collected during the sampling period, whereas the values for soil and bedrock water represent the water content-weighted mean isotopic value (Snyder and Williams, 2003) of the soil layer (0–40 cm) and bedrock layer (>40 cm), respectively.

Statistical analyses were conducted using the program SPSS 13.0 (SPSS Inc., Chicago, IL, USA). Stem water content and xylem isotopic data were subjected to the Student's *t*-test to detect significant differences ($P < 0.05$) between early and peak dry season or between the plant species. Within the *C. wightii* species, stem water content and xylem isotopic data were analysed by using the Student's *t*-test to detect any differences between adult trees and seedlings.

RESULTS

At the early dry season in November 2004, *C. sumatranus*, *L. comberi* var. *pseudoverticillat, C. wightii* adult trees and *C. wightii* seedlings showed similar average stem water contents (Table I). As the dry season progressed without precipitation, stem water contents for all species decreased significantly at the peak of the dry season ($P < 0.05$). However, *C. wightii* seedlings showed a much sharper decrease than adult trees. Xylem water δ^{18}O value did not differ significantly among the adult tree species at each sampling date ($P > 0.05$) but were different between adult trees and seedlings with seedlings being isotopically more enriched ($P < 0.001$). The δD value of xylem water in *C. sumatranus* was significantly higher than those of *L. comberi* var. *pseudoverticillata* and *C. wightii* ($P < 0.05$). Similarly, *C. wightii* seedlings showed significantly higher δD value compared with all adult tree species. In addition, xylem water isotopic value remained nearly unchanged between the two sampling events in each adult tree species. In contrast, isotopic value for *C. wightii* seedlings was more enriched in March 2005 than in November 2004. This result suggests that utilization of water sources subject to progressively greater evaporative isotopic enrichment.

Rainfall amount for 2004 was 1306 mm, which is slightly lower than the long-term average annual rainfall of 1454 mm (Figure 1(b)). Total rainfall for the 2005 dry season (from November 2004 through April 2005) was 55 mm, which is about 70% lower than the long-term mean for this period (191.3 mm). During this dry season, there were more than 4 months without any rainfall, and radiational fog were the only source of water input into the ecosystem. SWC was different at different depth at the peak of the dry season (Figure 2). Average water content was 16.7 ± 1.2% near the soil surface (0–3 cm), decreased to 15.9 ± 1.5% at 20 cm and increased again to 19.3 ± 0.5% at 50 cm. Below 50 cm depth, water content of bedrock remained relatively constant down to the maximum sampling depth. Large standard errors of SWC near the soil surface were observed, which reflects the great

Table I. Stem water content and isotopic value of xylem water in three adult tree species and one species seedling at the early (November 2004) and the peak (March 2005) of the dry season in the seasonal tropical rainforest.

	Stem water content (%)		Xylem water δ^{18}O (‰)		Xylem water δD (‰)	
Species	November	March	November	March	November	Marmarch
C. sumatranus	45.4 ± 0.5^{a}	36.9 ± 0.7^{a}	-7.0 ± 0.7^{a}	-6.5 ± 0.8^{a}	-53.6 ± 2.2^{a}	-50.1 ± 1.9^{a}
L. comberi var. *pseudoverticillata*	43.5 ± 0.7^{a}	35.2 ± 1.3^{a}	-7.7 ± 0.3^{a}	-7.5 ± 0.3^{a}	-61.8 ± 1.5^{b}	-59.4 ± 2.1^{b}
C. wightii	44.2 ± 0.4^{a}	35.9 ± 0.5^{a}	-7.4 ± 0.7^{a}	-7.1 ± 0.3^{a}	-56.3 ± 2.2^{b}	-55.1 ± 3.2^{b}
C. wightii seedling	43.8 ± 0.9^{a}	32.4 ± 0.6^{b}	-5.2 ± 0.5^{b}	-2.9 ± 0.7^{b}	-34.4 ± 2.3^{c}	-22.7 ± 1.8^{c}

Means ± standard errors are shown for all variables. Values in the same column followed by different normal letters are significantly different ($P < 0.05$).

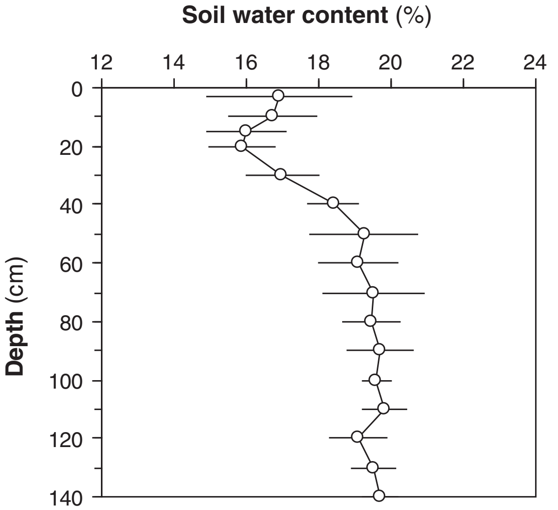

Figure 2. Water content in the soil/bedrock profile in the seasonal tropical rainforest at the peak (March) of the dry season in 2005. Values at each depth represent the average and standard error of six soil/bedrock samples collected from the sidewalls of two pits excavated.

heterogeneity of soil water condition, partially attributed to the irregular spatial distribution of drip point (where fog drip or light rain becomes concentrated because of peculiarities in the configuration of the trees and canopy) interspersed within the forest floor during the dry season (Bruijnzeel, 2001; Liu *et al*., 2004). Water content values in weathered bedrock also showed large standard errors, reflecting the extreme heterogeneity of the substrate composed of soil pockets interspersed within an intricate matrix of limestone bedrock. Soil water isotopic values were highest near the soil surface and decreased sharply with increasing depth to approximately 20 cm, then decreased slightly to about 60 cm depth, followed by nearly constant values down to the maximum sampling depth (Figure 3(a) and (b)). Fog drip isotopic value (volume-weighted) was consistently higher than those of all the concurrent soil/bedrock water samples and xylem water.

Xylem water δ^{18}O value ranged from −7.5 ± 0.3‰ in *L. comberi* var. *pseudoverticillata* adult trees to −2.9 ± 0.7‰ in *C. wightii* seedlings, whereas each corresponding δD value ranged from −61.8 ± 1.5 ‰ to −22.7 ± 1.8‰ (Figure 3(a) and (b)). This suggests that vertical partitioning of soil water sources would occur during the peak of the dry season. Xylem water samples deviated to the right of the local meteoric water line (δD = 7.96 and δ^{18}O + 8.67; Liu *et al*., 2005) (Figure 4), suggesting utilization of water sources subject to evaporative isotopic enrichment (Ehleringer *et al*., 1991; Williams and Ehleringer, 2000). The adult trees with the least isotopically enriched stem water exhibited δD and δ^{18}O values that closely matched the limestone bedrock water. By contrast, stem water in *C. wightii* seedlings plotted between soil water and fog water. As shown in Figure 3, mean isotopic values for xylem water and soil/bedrock water overlapped at a single depth range, enabling relatively accurate inferences of depth of water extraction by roots for the sampled species (Sternberg and Swart, 1987; Ehleringer *et al*., 1991). Water extraction appeared to be largely restricted to the upper soil layer in *C. wightii* seedlings (around 10 cm depth), whereas *C. sumatranus*, *L. comberi* var. *pseudoverticillata* and *C. wightii* adult trees seemed to be acquiring a greater proportion of deep water sources from the fractured limestone bedrock. According to the IsoSource model calculations, adult trees of all the three species primarily utilized water

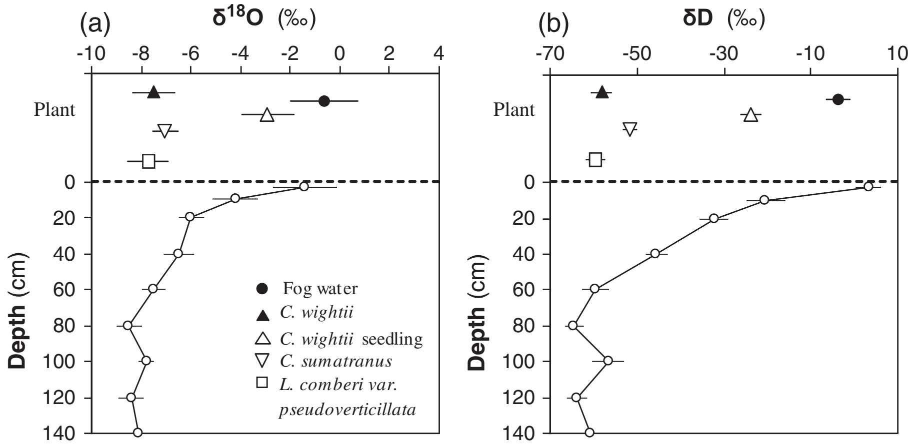

Figure 3. Average isotopic composition profile of soil/bedrock water and isotopic values of xylem water in three adult tree species and one species seedling at the peak (March) of the dry season in 2005 at the experimental site. Average isotopic values of fog water (n = 6) collected at the experimental site are also shown. Xylem water samples were collected on three adult trees per species but on five individuals for seedling. Values at each depth represent the average and standard error of six soil/bedrock samples collected from the sidewalls of the pits. Horizontal crossed bar represents ± 1 standard error.

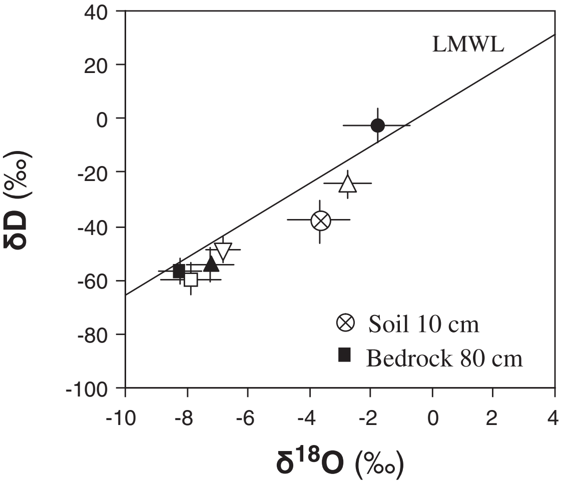

Figure 4. δD versus δ^{18}O values of xylem water in the three tree species, one species seedling, soil/bedrock water and fog water at the peak (March) of the dry season in 2005 at the seasonal tropical rainforest. Symbols mean the same as in Figure 3. Crossed bar represents ± 1 standard error. Fitted line is the local meteoric water line (LMWL; Liu *et al.*, 2005).

stored within the deeper, wetter locations within the limestone bedrock zone during the dry season (Table II), which is consistent with our initial assumption. *C. wightii* seedlings greatly relied on soil water and fog water, indicating that water from fog drip in the shallower soil horizons was an important source for seedling growth at the peak of seasonal drought.

DISCUSSION

Plant water sources

The large decreases in stem water content between November and April indicated that both adult trees and seedlings encountered a considerable water stress during the dry season (Table I). This result is consistent with a related study conducted at the same site (Wang *et al.*, 2008), which found that predawn leaf water potential (Ψ_{pd}) for the three species (*C. sumatranus*, *L. comberi* var. *pseudoverticillata* and *C. wightii*) was significantly lower at the peak of the dry season ($\Psi_{pd} = -0.25$, -0.40 and -0.42 MPa, respectively) than at the early dry season or rainy season ($\Psi_{pd} = -0.14$, -0.09 and -0.23 MPa, respectively). These results, as shown elsewhere (Flanagan *et al.*, 1992; Querejeta *et al.*, 2006, 2007; West *et al.*, 2007; Schwinning, 2008), suggested that groundwater was not a feasible source of water for these adult trees, because phreatophytic species tapping a permanent water table are usually well buffered from seasonal drought (Sternberg and Swart, 1987; Zencich *et al.*, 2002; Rose *et al.*, 2003). Although groundwater samples were not available in the experimental site, previous study in this area (Liu *et al.*, 2005) showed that groundwater had an average δ^{18}O value of -8.9 ± 0.6‰, which is slightly lower than that of the bedrock water sampled at the maximum sampling depth (-8.1 ± 0.4‰) but significantly lower ($P < 0.05$) than those of the xylem waters sampled. Deep perched water table in this site (>10 m; Li, 2008) and xylem water isotopic values of the adult trees that departed significantly from the groundwater isotopic signature also supported this interpretation. Groundwater utilization by woody vegetation under seasonally dry climates has often been shown to decrease with depth to the phreatic level, even when the strata overlying the aquifer are easier to penetrate by roots than limestone bedrock (Zencich *et al.*, 2002).

Results from the ISOSOURCE model revealed that adult trees of the three species were quite dependent on water stored within the weathered bedrock at the peak of the dry season (Table II). Even the *C. sumatranus* adult trees with the higher xylem water isotopic value derived around 62.5% of water from the bedrock, although the thin soil layer was also an important source of moisture (around 30.3%), which suggests a dimorphic root system. This would have resulted from a root system that preferentially acquires water from deeper bedrock water but can facultatively use shallow soil water, as shown elsewhere (Lin *et al.*, 1996; Jackson *et al.*, 1999; Hubbert *et al.*, 2001; Rose *et al.*, 2003; Oliveira *et al.*, 2005; Darrouzet-Nardi *et al.*, 2006).

All three species are evergreen, drought-tolerant species common in this seasonal rainforest, and all commonly present dimorphic rooting patterns, with surficial roots making up a greater bulk, but with some roots extending to greater depth (Li *et al.*, 1996). Although root density in the soil/bedrock profile was not quantified in this study, visual

Table II. Proportions of feasible water sources (%) for the different tree species in the seasonal tropical rainforest at the peak of the dry season in March 2005.

Water source	*C. sumatranus*	*L. comberi* var. *pseudoverticillata*	*C. wightii*	*C. wightii* seedling
Fog water	7.2 (2–14)	3.1 (1–6)	5.2 (0–10)	23.8 (13–41)
Shallow soil (0–40 cm)	30.3 (1–42)	11.9 (0–22)	15.7 (6–29)	61.6 (7–83)
Bedrock (>40 cm)	62.5 (45–72)	85.0 (73–91)	79.1 (66–84)	14.6 (0–47)

Average source proportions calculated by the ISOSOURCE mixing model (Phillips and Gregg, 2003) as the range of minimum/maximum source proportions are shown in parentheses.

inspection of pit sidewalls suggested that *C. sumatranus* adult trees possessed more lateral roots or surficial roots within the soil layer than the other two tree species. Visual observation also showed that some surficial roots for *C. sumatranus* adult trees extended more than 30 m in this forest. Greater lateral spread or higher density of roots in the thin soil layer could compensate for limited ability to access water stored within the limestone bedrock in this species. Better dry-season water status in *C. sumatranus* trees, as indicated by their higher stem water content (Table I) and higher midday leaf water potential ($\Psi_{\mathrm{md}} = -1.15$ MPa in *C. sumatranus* vs -1.87 MPa in *L. comberi* var. *pseudoverticillata* and -1.43 MPa in *C. wightii*; Wang *et al*., 2008), appeared to be the result of greater lateral root spread permitting exploration of larger soil/bedrock volume compared with the other two species. In addition, osmotic adjustment and the consequent ability to use soil water held at relatively low water contents are traits common to the *C. sumatranus* species (Wang *et al*., 2008). Sap flow measurements for the three tree species (*C. sumatranus*, *L. comberi* var. *pseudoverticillata* and *C. wightii*) indicated that maximum sap flow density (F_{m}) at the peak of the dry season was significantly decreased compared with that of the rainy season. The daily total sap flow measured in the dry season represented only 51%, 36% and 43% of the corresponding values measured in the rainy season for these three species, respectively (Wang, 2008). This suggested that *C. sumatranus* trees experienced less water stress than the other two species.

Meinzer *et al*. (1999) pointed out that the extensive horizontal area explored by roots system of canopy trees may partially compensate for the reduced water content in the upper portion of the soil profile, and soil water partitioning in canopy trees may reflect a necessary trade-off resulting from higher nutrient demand associated with maintenance of an extensive crown leaf area. However, maintaining roots in near-surface soils may provide limited benefits to plants under seasonally dry climates with unreliable moisture availability during the prolonged dry season (Drake and Franks, 2003; Querejeta *et al*., 2006; Goldstein *et al*., 2008). This is also confirmed by low water utilization in thin soil layer for adult trees of the three species (Table II). Additionally, some roots within the shallow soil layers might become inactive for the sampled species because the upper soil was greatly depleted in moisture during the peak of the dry season.

The about-2-year-old *C. wightii* seedlings exhibited mean isotopic values closer to the values of the shallowest soil layer and more enriched than values in the other soil/bedrock layers (Figure 3(a) and (b)). This is quite consistent with the visual inspection during sampling because active roots of seedlings were mainly restricted to the upper 10 cm depth of the soil. Output from the mixing model indicated that the proportion of water obtained by seedlings from fog drip was around 23.8% (Table II). This result suggested that water from fog drip in the shallower soil horizons was an important source for seedling growth at the peak of seasonal drought. This is likely because seedling root biomass was greatest in shallow horizons where uptake of fog moisture inputs would be most efficient, as previously shown by Corbin *et al*. (2005). An earlier study at a nearby rainforest site (Liu *et al*., 2005) also pointed out that the shallower soil water, which had isotopic composition usually between those of the rain and fog drip, was a mixture of the two water sources. This suggested that seedlings obtained their water from the shallower soil layer, where water appeared to be a mixture of frequent fog drip and previous soil water provided primarily by recent rainfall recharge events.

In consistent with the long drought period, stem water content of *C. wightii* seedling was significantly lower at the peak dry season than at the early dry season or in comparison with adult trees of the same species at the peak dry season (Table I). This suggested that seedlings experienced more severe water stress than adult trees. This is consistent with information from a related study at this site that suggested *C. wightii* seedlings are very sensitive to water availability (Li *et al*., 1996).

In contrast, adult trees of the three sampled species had little or negligible water uptake from fog moisture (3–7% on average) during the dry season. In fact, daily fog drip (<1.0 mm) can only infiltrate a few centimetres of the topsoil (Liu *et al*., 2005), and fog uptake by these adult trees through their deeper lateral roots should be quite limited. Dawson (1998) hypothesized that smaller trees and understory species use more fog water than larger trees, which is consistent with rooting depth information because smaller trees possess a greater fraction of shallow roots and may therefore use a greater proportion of shallow soil water that originated from fog drip. Our results tend to strongly support this hypothesis. Similarly, Corbin *et al*. (2005) found that the most likely zone of active water use from fog during dry season drought was at around 10 cm depth, where plants could take advantage of the frequent moisture inputs from fog. However, it must be pointed out that direct fog uptake through foliage may also be important although it is likely a much smaller fraction than that taken up through roots (Burgess and Dawson, 2004), but this was not quantified here. Hence, our estimates of fog use by plants may be conservative.

Implications

It has been suggested that the distribution of certain vegetation types may be heavily reliant on the frequent fog moisture inputs (Bruijnzeel, 2001; Burgess and Dawson, 2004). Fog water can contribute directly to water use by plant roots or leaves, but it may influence plant water balance in other ways as well. Decreased evapotranspiration due to reduction of the number or hours of sunshine and moderate day/night time temperature during fog events relieves plant water stress (Dawson, 1998; Burgess and Dawson, 2004; Liu *et al.*, 2004; Corbin *et al.*, 2005). Ritter *et al.* (2009) demonstrated that the whole aerial environment was altered by foggy conditions, and basic physiological processes of the plants were greatly affected. These features were also noted by Hutley *et al.* (1997) in an Australian subtropical rainforest, and their results showed that the frequent occurrence of fog and wet canopy resulted in reduced transpiration rates and direct foliar absorption of moisture during the dry season. Moreover, it is worth noting that frequent wetting and direct uptake of water by canopy leaves may have consequences for cambial development and could result in complex patterns of xylem development and branch hydraulic resistances (Burgess and Dawson, 2004).

In our study, seedlings suffered a stronger water stress and greatly relied on available moisture from fog drips, although it could not fully meet the water requirements of seedlings. The ability to take up a greater proportion of upper soil water that is mostly from fog drip during the pronounced dry season is likely the key feature allowing *C. wightii* seedlings to thrive. A related study on seed germination and seedling growth in this forest site showed that *C. wightii* seeds had low dehydration tolerance and appeared to germinate anywhere in the forest, with high germination rate and high seedling mortality percentage (Li *et al.*, 1996). However, after 4–5 years of growth, young trees can grow roots quickly into the bedrock layer and could use the reliable deep soil/bedrock water sources (Liu, personal observation). This strategy enhanced the probability of successful regeneration for this species in the ecosystem. Moreover, *C. wightii* seedlings grew better in small forest gaps, where there was more fog drip owing to ‘drip point effect’ (Bruijnzeel, 2001) and higher diffuse radiation (Cai *et al.*, 2009).

As mentioned previously, *C. wightii* seedlings greatly relied on available fog water at the peak dry season compared with the early dry season, suggesting that seedlings may encounter a greater water stress during a drier-than-average dry season/year, such as that in 2005, compared with average or wet years. An earlier study also pointed out that more abundant fog drip during dry years implies that fog water is more important in sustaining this forest throughout the dry season (Liu *et al.*, 2004). Similarly, Dawson (1998) demonstrated that plant dependence on fog water was higher in the dry years than during an average climatic year at a redwood forest site in California. Because both seedlings and shallow-rooted understory species require moisture and cool conditions to regenerate in the forest (Cai *et al.*, 2009), it might be expected that some other tree seedlings and understory species also partially rely on fog moisture in the forest during the dry season, but further research focusing on each of these possibilities is needed.

During the past several decades, climate change has occurred in this tropical region, decreasing the annual number of fog events and duration and warming temperatures (Li, 2001). Liu *et al.* (2004) proposed that the observed climate change in this region could be partially attributed to the extensively large-scale deforestation (mainly converting rainforest to rubber plantation). There is an increasing body of work suggesting that substituting primary forest for farmland or other land use might greatly alter the water balance and consequently the local and regional-scale climate (Bruijnzeel, 2001). There is also a report that large-scale deforestation could reduce cloud/fog formation and increase cloud-base height (Lawton *et al.*, 2001). These results would reasonably suggest that converting dense multilayer forest into other land use and land cover patterns in our study region will reduce fog formation and duration and may have far-reaching negative impacts on this limestone forest ecosystem (such as seed germination and seedling growth). For example, some species seedlings or shallow-rooted understory species that partially depend upon the moisture input from fog drip or other microclimatic benefits caused by the presence from fog could experience more frequent water stress or even suffer high rates of mortality if inputs of fog water had declined.

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