

Dry season water uptake by two dominant canopy tree species in a tropical seasonal rainforest of Xishuangbanna, SW China

Wenjie Liu^{a,*}, Wenyao Liu^a, Pengju Li^{a,b}, Wenping Duan^a, Hongmei Li^a

^aXishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, Kunming 650223, PR China

^bGraduate School of the Chinese Academy of Sciences, Beijing 100039, PR China

ARTICLE INFO

Article history:

Received 17 July 2009

Received in revised form 17 December 2009

Accepted 21 December 2009

Keywords:

Dry season

Fog water dripping

Seedling growth

Stable isotopes

Tropical rainforest

Water uptake

ABSTRACT

Radiation fog has been suggested as an important source of moisture in tropical seasonal rainforest of Xishuangbanna during 6 months of annual drought, yet its importance for the plants which inhabit this ecosystem is virtually unknown. We assessed patterns of water uptake by two major seasonal rainforest canopy tree species in Xishuangbanna, SW China, during two consecutive dry seasons (2005 and 2006). Stable oxygen isotope compositions of water in xylem, soil, fog, rain, and groundwater were analyzed, and soil water content and leaf water potential were measured concurrently in order to determine the proportion of water deriving from shallow soil by mature trees and from fog water by seedlings during the pronounced dry season. Our results indicated that evergreen *Gironniera subaequalis* tree appeared to be acquiring water preferentially from the upper 50 cm of the soil profile, with around 53–72% of its water from shallow soil. In contrast, brevi-deciduous *Pometia tomentosa* tree seemed to be tapping water mostly from depths greater than 60 cm or from groundwater, with about 28–46% of its water from shallow soil, suggesting that it relies predominantly on its deep taproot for water uptake. During the dry season, when fog was most frequent, 23–59% of the water used by *P. tomentosa* seedling came from fog water after it had dripped from tree foliage into the soil, indicating that fog water was an important source for seedling growth, especially at the peak of the dry season. Since both seedlings and shallow-rooted understory species require moisture and cool conditions to regenerate, it might be expected that some other tree seedlings and understory species also partially rely on fog moisture during the pronounced dry season, but further research is needed.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Water is a critical resource that limits the distribution and abundance of vegetation in the world. 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; Meinzer et al., 1999; Goldstein et al., 2008). Therefore, the distribution and accessibility of soil water greatly influences plant growth and survival (Drake and Franks, 2003). 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). 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). 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; Schnitzer, 2005; Goldstein et al., 2008) and within similar growth forms (Thorburn et al., 1993; Field and Dawson, 1998; Meinzer et al., 1999; Pate and Dawson, 1999; Stratton et al., 2000). However, it is difficult to draw inferences about spatial partitioning of soil water in tropical forests based on direct observation of rooting patterns because of the large and intricate root biomass, high species diversity characteristic of these ecosystems, and 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., 2000). 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; Dodd et al., 1998; Dawson et al., 2002).

Water from fog has been shown to constitute a significant portion of the total hydrologic inputs in a number of terrestrial

* Corresponding author at: Kunming Section, Xishuangbanna Tropical Botanical Garden, 88 Xuefu Road, Kunming 650223, PR China. Tel.: +86 871 5160910; fax: +86 871 5160916.

E-mail address: lwj6932002@yahoo.com.cn (W. Liu).

ecosystems (Bruijnzeel, 2001). However, few studies have quantified the degree to which vegetation relies on fog water (but see Ingraham and Matthews, 1995; Dawson, 1998; Field and Dawson, 1998; Burgess and Dawson, 2004; Corbin et al., 2005). One of the best studies is Dawson's research on coastal redwood forests in California, where 8–42% of the water obtained by redwood trees and 6–100% of the water obtained by understory species was derived from fog (Dawson, 1998).

Within the tropical seasonal rainforest of Xishuangbanna, SW China, most plants remain evergreen and continue to transpire during dry season months (November–April) when rain is sparse. Previous study (Liu et al., 2004) showed that in this forest stand the absolute average amount of annual fog water dripping was 89.4 mm, which contributes an estimated 5% of the annual rainfall, with 86% of the fog water dripping occurring in the dry season. This means fog in Xishuangbanna is of particular ecological significance, because the period of most frequent fog occurring coincide with the dry season drought. While it is reasonable to expect that plants inhabiting the tropical seasonal rainforest might use fog water and that fog plays an important role in the existence of the rainforest in this area (Cao et al., 1996), no work had been done to test if this was true and to quantify the extent to which fog water dripping is used by plants.

The objective of this study was to determine the dry season patterns of water source use for two dominant canopy tree species, *Pometia tomentosa* and *Gironniera subaequalis*, in a tropical seasonal rainforest of Xishuangbanna, by sampling the stable O isotope ratios of water in soil, fog, rain, groundwater and non-photosynthetic tissue, and measuring gravimetric soil water content and leaf water potential, during two consecutive dry seasons (2005 and 2006). Specifically, we tested the use of fog water dripping by *P. tomentosa* seedlings. We hypothesized that: (i) mature canopy trees utilize water primarily from greater depths in the soil profile, (ii) evergreen *G. subaequalis* taps deeper sources of water whereas brevi-deciduous *P. tomentosa* obtains water from shallower soil layers, and (iii) tree seedlings, whose roots are limited to the uppermost soil layer, would use much more water from fog, thus circumventing the problem of limited water supply from the uppermost soil during the dry season.

2. Materials and methods

2.1. Study site

The study was conducted at a tropical seasonal rainforest site (21°55'39"N, 101°15'55"E, 750 m a.s.l.) in Menglun town of Xishuangbanna in southwestern China. This site is located on a small flat area between two hills extending from east to west, and is a permanent plot (dominated by *P. tomentosa* and *Terminalia myriocarpa*) dedicated to the long-term ecological research managed by the Tropical Rainforest Ecosystem Station, the Chinese Academy of Sciences. This type of forest is primarily formed in wet valleys, lowlands and on low hills where heavy radiation fogs frequently occur (Cao et al., 1996). A stream (about 1 m wide) winds through the study site. Slope to the south and north of the site is about 15°. The soil under the forest is yellow a latosol developed from purple sandstone. This forest is a kind of tropical rainforest, which, however, differs from lowland tropical rainforest in that some of its tree species are deciduous under the monsoon climate, although they do not shed leaves in the same season. More detailed information about the forest is provided by Cao et al. (1996).

The Hengdwan Mountains to the north of the region act as a major barrier keeping out cold air coming from the north in the winter. Between May and October (rainy season), the tropical Southwest Monsoon from the Indian Ocean delivers about 85

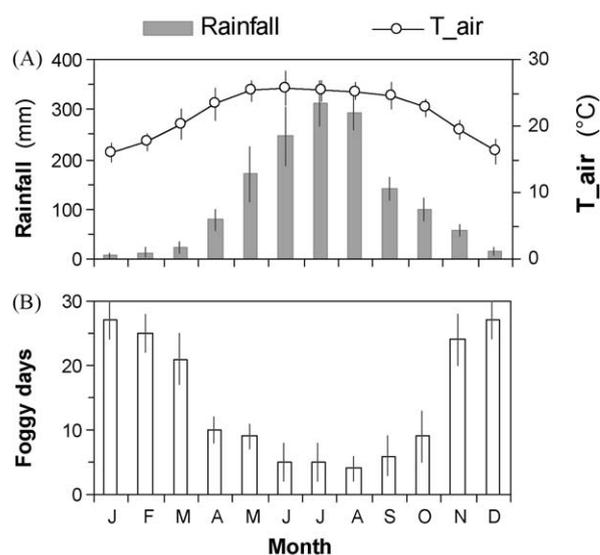


Fig. 1. Average monthly rainfall and air temperature (A), and foggy days (B) at a weather station nearby the experimental site. Each vertical bar represents an average (± 1 SE) for that month calculated from records during 1965–2004 for rainfall and temperature, and during 1998–2004 for foggy days.

percent of the annual rainfall, whereas the dry and cold air of the southern edges of the subtropical jet streams dominates 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 morning, and a hot sub-season from March to April, which is characterized by dry and hot weather during the afternoon and with radiation fogs during the morning only (Fig. 1B). 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 season (Liu et al., 2004).

Long-term climate records as measured at a nearby weather station 5 km southeast from the study site in the past 40 years shows 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, and are always associated with a low relative humidity (less than 40%). The mean annual rainfall is 1487 mm, of which 87% occurs in the rainy season vs. 13% in the pronounced 6-month dry season (Fig. 1A). 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 m s⁻¹ (Liu et al., 2004).

2.2. Water, vegetation, and soil sampling

Water samples for isotope analysis were collected from fog water dripping, rain, groundwater, plant xylem water and soil water. Six v-shape troughs (0.3 m × 2.0 m), each connected to a plastic bottle, were mounted 0.7 m above the forest floor and were placed in a random pattern to collect fog water dripping from the canopy. Fog water dripping sampling was performed weekly at predawn, at or near the peak of a fog water dripping event, but before isotopic fractionation had occurred from re-evaporation (Dawson, 1998). During the dry season, only 10% of the annual rainfall occurs from relatively few storms, and days with night rain generally do not have radiation fog the following morning (Liu et al., 2004). Hence, water collected by the troughs comes from fog water dripping only. Three hand-dug wells were installed near the

fog drip sampling sites and groundwater samples were collected from these wells at monthly intervals. Daily fog drip amounts and monthly water table depths were measured from November 2004 to April 2006.

During the study period, rain samples were collected at each rain event when rainfall exceeded 5 mm at the weather station. Samples of rainfall were collected immediately after rainfall ceased, or in the early morning when rain fell overnight. Samples of rain, fog water dripping and groundwater were stored in sealed screw-cap borosilicate glass vials, wrapped in Parafilm, and frozen (-20°C) until later analysis.

Plant and soil water were sampled at the early (December) and the peak (March) of the dry season during 2004/2005 and 2005/2006. Sampling dates were 2 December 2004, 30 March 2005, 18 December 2005, and 23 March 2006. On each sampling date (at midday), plant xylem samples were obtained from each of the 3 selected mature trees for brevi-deciduous *P. tomentosa* and evergreen *G. subaequalis*, respectively. For each sample, xylem tissues 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 each of 3–5 randomly *P. tomentosa* seedlings (<2 years old, <15 cm high) that emerged nearby the mature trees during the 2005 dry season. Seedling xylem samples for *G. subaequalis* were not collected because there were not sufficient seedlings for subsequent analysis. 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 (whether from fog or rain) taken up by roots, rather than directly by foliage (Dawson, 1998; Ehleringer et al., 2000; Corbin et al., 2005). In addition, the midday leaf water potentials (Ψ_{md}) of 3–4 leaves from individuals of each species and from seedlings were measured using a pressure chamber (Pump-Up Pressure Chamber, PMS instruments, USA). For Ψ_{md} and isotope determinations, the same mature trees were sampled repeatedly on successive dates. While for seedlings, sampling on 2 December 2004 used most of the available tissue and effectively killed the plants. As a result, subsequent 2005 sampling used replacement individuals of the same size and in the same approximate locations as the initial plants.

Simultaneously with plant sampling, soil samples were collected with a bucket auger from each of eighteen depths (shown on the vertical axis of Fig. 3) from a borehole located beneath each of the selected mature trees. Soil water content (SWC, %) was determined from the sample weight loss by drying all samples at 105°C for 24 h. At the same time, the isotopic gradient in the soil profile was sampled by taking sequential soil cores (3, 10, 20, 40, 60, 80, 100, 120, and 150 cm depths). The isotopic composition of plant xylem water was assumed to be an integrated measure of the water in the soil horizons from which plant actively took up water, and was compared to the gradient of isotopic values through the soil profile (Ehleringer et al., 2000). Soil and plant tissue samples were stored as described above, 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 O isotopic composition of all water samples was determined using a 5-day equilibration of water samples with CO_2 followed by mass spectrometer analysis (Finnigan MAT252, Bremen, Germany) at the Test Center of Lanzhou Branch, the

Chinese Academy of Sciences. Isotope ratios ($\delta^{18}\text{O}$) are expressed in ‰ relative to V-SMOW (Vienna standard mean ocean water; Ehleringer et al., 1991).

We use $\delta^{18}\text{O}$ values of rain, fog water dripping, soil water, groundwater and xylem water to analyze plant water uptake during the dry season. The percentage of water from shallow soil used by mature trees, and from fog used by seedlings was estimated with a two-end-member mixing model (White et al., 1985; Dawson, 1998). This model needs some assumptions, e.g. that there are only two dominant water sources for our each situation. For mature trees, shallow soil (<60 cm) and deep soil (≥ 60 cm) were considered as the two dominant water sources based on rooting depth estimates by visual inspection and analysis of soil $\delta^{18}\text{O}$ profile (see below). The model is as follows:

$$F = \frac{\delta^{18}\text{O}_{\text{plant}} - \delta^{18}\text{O}_{\text{deepsoil}}}{\delta^{18}\text{O}_{\text{shallowsoil}} - \delta^{18}\text{O}_{\text{deepsoil}}} \quad (1)$$

where $\delta^{18}\text{O}_{\text{shallowsoil}}$ is the water content-weighted (Dawson, 1998; Snyder and Williams, 2003) mean $\delta^{18}\text{O}$ value of the upper soil layer (<60 cm), and $\delta^{18}\text{O}_{\text{deepsoil}}$ is the water content-weighted mean of the below-60 cm soil $\delta^{18}\text{O}$ values.

This mixing model assumes that each of the two water sources is homogenous. Because shallow soil $\delta^{18}\text{O}$ was graded instead of homogenous, we cannot estimate the exact percentage of soil water that each plant acquired from shallow soil. However, the deep soil was homogenous so we can estimate the minimum percentage of soil water (minimum F) that each plant acquired from shallow (<60 cm) soil (after Phillips and Gregg, 2001; Darrouzet-Nardi et al., 2006). The percentage of water from fog used by mature trees through roots was not considered because the studied mature tree roots were restricted to mainly below 15 cm depth of the soil profile (Liu, personal observation; Muthukumar et al., 2003), where uptake of fog water would be impossible since daily fog drip (<1 mm) can only infiltrate a few centimeters of the topsoil. Our previous study (Liu et al., 2005) showed that during the dry season the fog water pulse was only detected down to a depth of a few centimeters of the topsoil (by using isotope as tracer).

For seedlings, $\delta^{18}\text{O}_{\text{shallowsoil}}$ in this model is the volume-weighted mean $\delta^{18}\text{O}$ value for fog water dripping ($n=4-6$) collected before each sampling event. $\delta^{18}\text{O}_{\text{deepsoil}}$ is the mean $\delta^{18}\text{O}$ value of rain ($n=4-13$; collected during each dry season) and topsoil water (<20 cm), which was determined by combining the volume-weighted mean $\delta^{18}\text{O}$ value of rain with the water content-weighted mean of $\delta^{18}\text{O}$ value from the topsoil water, and dividing this value by 2 (adapted from Dawson, 1998).

Statistical analyses were conducted using the SPSS 13.0 program. SWC, Ψ_{md} , and $\delta^{18}\text{O}$ data of soil and xylem water were subjected to the Student's t -test in order to detect significant differences ($P < 0.05$) between the early and the peak of the dry season, or between the two tree species. Within the *P. tomentosa* species, leaf water potential and $\delta^{18}\text{O}$ data of xylem water were analyzed by Student's t -test to detect stage differences between mature tree and seedling. Volume-weighted mean isotopic composition was calculated for rain and fog water dripping, and water content-weighted mean isotopic composition was calculated for shallow (<60 cm) or deep (≥ 60 cm) soil water.

3. Results

3.1. Seasonal rainfall and groundwater level

Total rainfall for 2005 and 2006 was 1429 and 1456 mm, respectively, similar to the 40-year mean (1965–2004), but the seasonal patterns were somewhat different from the means (Fig. 2).

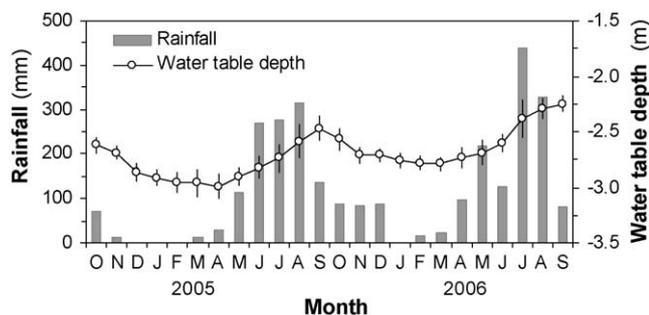


Fig. 2. Monthly rainfall distribution and groundwater table level during October 2004–September 2006 period at the experimental site. Vertical bar represents ± 1 SE ($n = 3$).

Rainfall amount for 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; Fig. 1A), with a dry spell of more than 4 months without any rainfall. For 2006 dry season, it was 306 mm, about 60% higher than the mean. Groundwater levels generally declined throughout each of the sampling dry periods. The lowest water table was -2.99 m, which occurred at the peak of the 2005 dry season. For the early through the peak of the dry season, the water table was below the deepest depth for all soil water sampling.

3.2. Soil moisture and isotopic composition

Soil water content (SWC) underwent pronounced seasonal changes down to 160 cm depth during both the dry seasons (Fig. 3). The difference of SWC between the early and the peak of the dry season was significantly higher in 2005 than in 2006 in the upper 60 cm soil layer ($P < 0.001$), whereas similar difference was observed below 60 cm depth. At the peak of the 2005 dry season, SWC increased sharply with depth from about 17% near the soil surface (0–3 cm) to 26% at 60 cm layer, then remained relatively constant down to the maximum sampling depth of 160 cm (Fig. 3A). However, the increase in SWC over the 40 cm between the 20 and 60 cm layer was relatively small compared to the increase between 0 and 20 cm. Similar patterns were also observed early in the 2005 dry season and during both the early part and the peak of the 2006 dry season, but with a relatively weak trend (Fig. 3B). Also, SWC at the peak of the dry season was significantly lower in 2005 than in 2006 in the upper 60 cm soil layer ($P < 0.01$), but no significant difference was found at depth below 60 cm ($P > 0.05$). Large SEs of SWC near the soil surface layer were also observed, which reflects the great heterogeneity of soil water

condition, partially attributed to the irregular spatial distribution of 'dripping points' (where fog water dripping or sparse light rain becomes concentrated because of specific features in the configuration of the trees and canopy) interspersed within the forest floor during the dry season (Liu et al., 2004).

Generally, soil water $\delta^{18}\text{O}$ 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 (Fig. 4). For all sampling events, the $\delta^{18}\text{O}$ values at the deepest soil depths were close to the value of the concurrent groundwater samples, which had an average value of $-8.8 \pm 0.5\text{‰}$ ($n = 16$). At the early of the dry season sampling dates for 2005 and 2006, profile $\delta^{18}\text{O}$ values were similar within the sampling depth, but showed a greater enrichment near the soil surface (-2.1‰) in 2005 (Fig. 4A and C; $P < 0.01$). Also a discrete minimum in $\delta^{18}\text{O}$ values along the upper 40 cm soil profile occurred at the 2005 sampling date. This discrete minimum should be associated with a 29 mm rain event 12 days before the sampling date. The isotopically enriched signature of this rainfall (-4.3‰) was modified deeper in the profile as it infiltrated through the surface and became less enriched as it mixed with older water in the soil profile.

Across all the sampling events, the greatest enrichment occurred in the soil profile at the peak of the 2005 dry season, where maximum value approached -1.9‰ near the soil surface (Fig. 4B). A similar pattern was also observed in March 2006, but with $\delta^{18}\text{O}$ values near the soil surface (-2.8‰) significantly lower than that in 2005 (Fig. 4D; $P < 0.001$). Volume-weighted mean $\delta^{18}\text{O}$ value of rain was significant higher for the 2005 dry season ($-4.1 \pm 1.2\text{‰}$) than for the 2006 dry season ($-5.2 \pm 0.7\text{‰}$; $P < 0.01$). Fog water dripping $\delta^{18}\text{O}$ values (volume-weighted) were consistently higher than those of rain samples, all the concurrent soil water samples and xylem waters (see below), and ranged from -2.5 to -1.2‰ , with the highest value also occurring at the peak of the 2005 dry season (Fig. 4B).

3.3. Isotopic composition of xylem water and depth of water uptake

We observed a consistent trend in $\delta^{18}\text{O}$ values across the two species (Fig. 4), with mature trees of *P. tomentosa* having the lowest $\delta^{18}\text{O}$ values (-7.9 to -6.6‰), and *P. tomentosa* seedling displaying the highest $\delta^{18}\text{O}$ values (-3.4 to -2.5‰). *G. subaequalis* $\delta^{18}\text{O}$ values were intermediate and ranged from -6.8 to -5.2‰ . $\delta^{18}\text{O}$ values for *P. tomentosa* seedlings were significantly higher than those for both of the studied trees ($P < 0.001$), with the highest value (-2.5‰) occurring at the peak of the 2005 dry season (Fig. 4B). SEs in $\delta^{18}\text{O}$

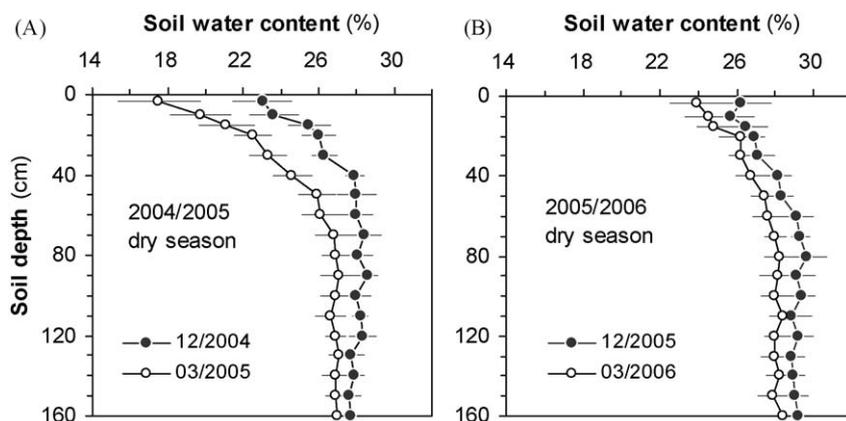


Fig. 3. Vertical profiles of mean gravimetric soil water content at the early (December) and the peak (March) of the dry season in 2005 (A) and 2006 (B) at the experimental site. Horizontal crossed bar represents ± 1 SE ($n = 3$).

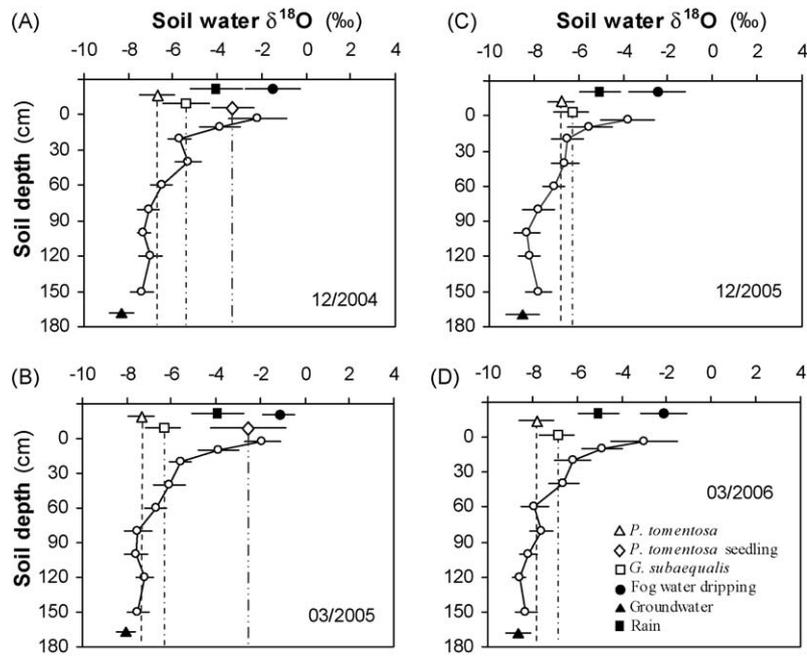


Fig. 4. Average $\delta^{18}\text{O}$ isotopic profile of soil water and $\delta^{18}\text{O}$ values of xylem water (mean \pm SE) in two tree species and one seedling at the early (December) and the peak (March) of the dry season in 2005 (A and B) and 2006 (C and D) at the experimental site. Average $\delta^{18}\text{O}$ values of fog water dripping (volume-weighted; $n = 4\text{--}6$), groundwater ($n = 3$) and rain (volume-weighted; $n = 4$ for the 2005 dry season; $n = 13$ for the 2006 dry season) collected at the experimental site are also shown. Horizontal crossed bar represents ± 1 SE. Xylem water samples were collected on 3 trees per species (*P. tomentosa* and *G. subaequalis*), but on 3–5 individuals for seedling xylem water of *P. tomentosa*. Soil water $\delta^{18}\text{O}$ values are means of three holes.

values of xylem water for each sampling event were typically less than 1.0‰, with the exception of higher variability (up to 1.4‰) for *P. tomentosa* seedling which reflects a great heterogeneity of plant water source.

Xylem water $\delta^{18}\text{O}$ values can provide an integrated estimate of water uptake by roots, and by comparing these values to $\delta^{18}\text{O}$ values of potential water sources, it is possible to determine the main water source used by a plant (Sternberg and Swart, 1987; Ehleringer et al., 1991; Jackson et al., 1999). As shown in Fig. 4, mean $\delta^{18}\text{O}$ values for xylem water and soil water overlapped at a single depth range for most sampling events, enabling relatively accurate inferences of depth of water extraction by roots for these two species. Xylem $\delta^{18}\text{O}$ values for the early of the 2005 dry season (Fig. 4A) suggest that trees obtained their water from about 60 cm depth for *P. tomentosa* and between 20 and 40 cm depths for *G. subaequalis*, whereas seedlings obtained water from about 5 cm depth. As the season progressed and no rainfall occurred during this period (i.e., peak of the dry season), depth of plant water uptake shifted to deeper levels in the soil profile for the two species (below 80 cm for *P. tomentosa* and around 50 cm for *G. subaequalis*), whereas no change occurred for the seedlings (Fig. 4B). The unchanged depth of plant water uptake suggests that *P. tomentosa* seedling still had a stable water source as the dry season progressed. During the 2006 dry season, significant rainfall occurred through November to December (170.6 mm, about 140% higher than the mean; Fig. 2), and at the early sampling (Fig. 4C), plant water uptake appeared to be largely restricted to a relatively shallow layer (around 40 cm for *P. tomentosa* and around 20 cm for *G. subaequalis*) under well-watered condition compared to the previous dry season. Similarly, depth of plant water uptake also shifted to deeper levels at the peak of the dry season (between 60 and 80 cm for *P. tomentosa* and around 40 cm for *G. subaequalis*; Fig. 4D).

3.4. Differences of water use by plants

In contrast to our hypothesis, brevi-deciduous *P. tomentosa* tree utilized water primarily from the hypothetical deepest zone, indicating that this species was functionally dimorphically rooted

and may have had access to a deeper water source throughout the dry season. *F* (percentage of water from shallow soil) of *P. tomentosa* ranged from 28% to 46%, suggesting that it relies predominantly on its deep taproot for water uptake (Fig. 5), even where there is an appreciable amount of upper soil moisture at the early of the 2006 dry season (Fig. 3). However, evergreen *G. subaequalis* was not restricted to using deep water throughout the dry season and seemed to have a large amount of roots capable of taking up water in the shallow soil (*F* ranged from 53% to 72%). As the dry season progressed and the upper soil layers gradually dried, depth of plant water uptake shifted to deeper and moister layers (Fig. 4), and *F* decreased consequently for both species.

For *P. tomentosa* seedlings, *F* (percentage of water from fog) was 23% and 59% at the early and the peak of the 2005 dry season respectively (Fig. 5C), suggesting that water from fog water dripping in the shallower soil horizons was an important source for seedling growth during the peak of the dry season.

3.5. Plant water potential

The midday leaf water potentials (Ψ_{md}) of the two species in the 2005 dry season were relatively low and increased in the wetter dry season of 2006 (Fig. 6), and the Ψ_{md} difference between 2005 and 2006 at the early or at the peak of the dry season was significant ($P < 0.01$). Compared to the early of the dry season, subsequently later dry spell caused Ψ_{md} to drop in both species. For each sampling event, *G. subaequalis* had slightly higher Ψ_{md} values than *P. tomentosa*, but the difference was not significant ($P > 0.05$), indicating that *G. subaequalis* developed a less water stress during the dry season. At the peak of the 2005 dry season, after a long-lasting drought (>4 months), Ψ_{md} value for *P. tomentosa* seedlings was significantly lower in comparison to mature trees of the same species ($P < 0.01$), with Ψ_{md} value of seedlings being -1.02 MPa, suggesting that *P. tomentosa* seedlings suffered greater water stress. Also, significant difference was found between the early and the peak of the dry season for seedlings ($P < 0.01$).

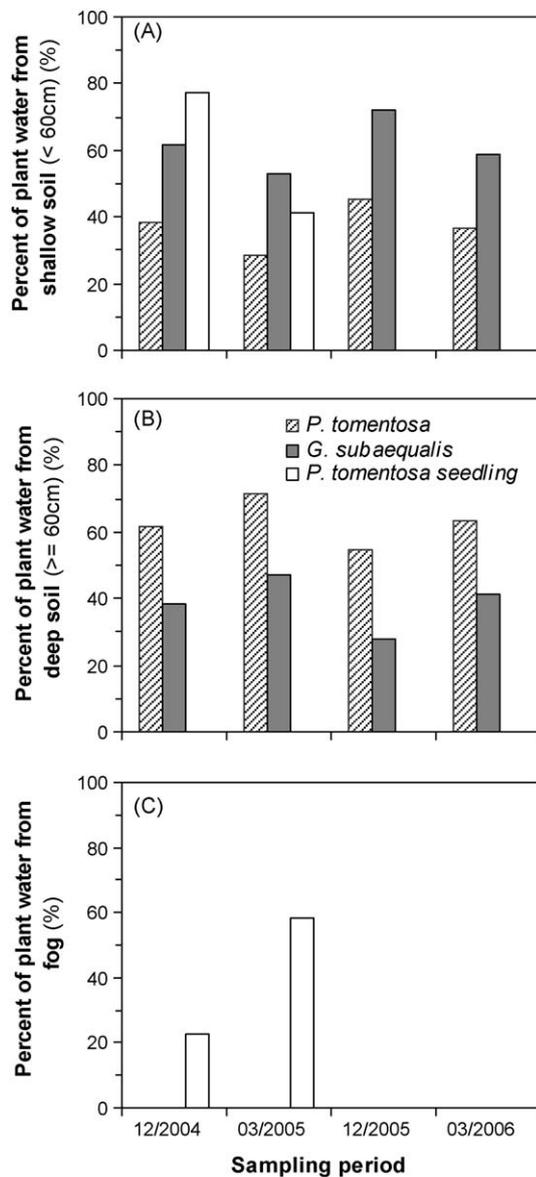


Fig. 5. Percentage of plant water uptake from shallow soil (A), deep soil (B) and fog water dripping (C; for seedling only) at the early and the peak of the dry season in 2005 and 2006 at the experimental site. The percentage of water used by plants was estimated with a two-end-member mixing model. See text for details.

4. Discussion

4.1. Seasonal patterns of plant water uptake

The results of this study indicated that soil water resources varied in time and space in the study site. SWC and groundwater level exhibited strong seasonality, consistent with the seasonal changes in rainfall amount (Figs. 2 and 3). Soil and xylem water $\delta^{18}\text{O}$ data revealed that, on average, evergreen canopy tree *G. subaequalis* appeared to be acquiring water preferentially from the upper 40 cm of the soil profile at the early of the dry season when soil water was relatively plentiful, and slightly increased its depth of water uptake (<50 cm) as the upper soil layers gradually dried and water became less available at the peak of the dry season (Figs. 3 and 4). Several other studies conducted in seasonally dry tropical ecosystems have also concluded that trees depend mostly on water stored within the upper soil/subsoil profile during the dry season (Drake and Franks, 2003; Andrade et al., 2005; Romero-

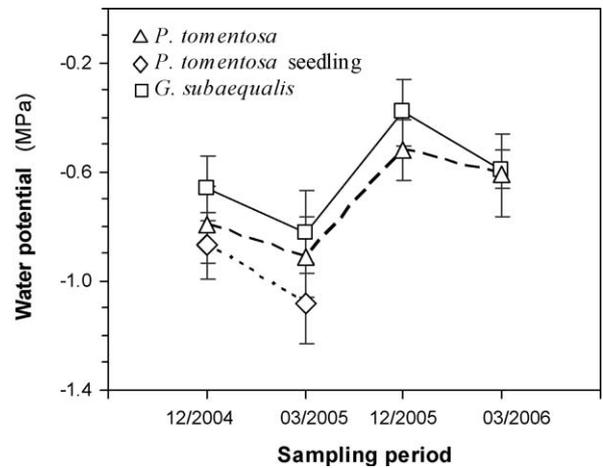


Fig. 6. Average midday leaf water potentials (Ψ_{md}) of the two tree species and one seedling at the early and the peak of the dry season in 2005 and 2006 at the experimental site. Vertical bars represents ± 1 SE ($n = 3-5$). Note that values of *P. tomentosa* seedling for the 2006 dry season and of *G. subaequalis* seedling for all the sampling events were not available since there were not sufficient individuals for subsequent analysis.

Salto et al., 2005; Nippert and Knapp, 2007; Goldstein et al., 2008). In contrast, brevi-deciduous *P. tomentosa* seemed to be tapping water mostly from depths greater than 60 cm where SWC was relatively constant, suggesting increased reliance on deeper soil water or even groundwater as the dry season progressed. An exception is that at the early of the 2006 dry season when significant rainfall occurred (about 140% higher than the mean) and SWC in the upper soil was higher, *P. tomentosa* also appeared to be acquiring water from the upper soil layer (<60 cm), indicating that *P. tomentosa* exhibited a high degree of plasticity in rooting depth. This resulted from a root system that preferentially acquires water from deeper soil but can alternatively use shallow soil water, as shown elsewhere (Ehleringer et al., 1991; Lin et al., 1996; Meinzer et al., 1999; Dawson et al., 2002; Ewe and Sternberg, 2002; Darrouzet-Nardi et al., 2006). This finding is also supported by our visual inspection of pit excavation just nearby the study site, indicating that *P. tomentosa* tree possesses both lateral roots and deeply penetrating taproots (Liu, personal observation). According to the two-end-member model calculations (Fig. 5), brevi-deciduous *P. tomentosa* with the least xylem water $\delta^{18}\text{O}$ derived around 54–72% of its water from deeper water sources throughout the dry season, whereas evergreen *G. subaequalis* obtained around 53–72% of its water from upper soil layers, consistent with the above analysis. This result, in contrast to previous studies (Jackson et al., 1995; Meinzer et al., 1999; Bonal et al., 2000), did not also support our initial assumption that evergreen *G. subaequalis* taps deeper sources of water whereas brevi-deciduous *P. tomentosa* obtains water from shallower soil layers. However, the ability to tap deep soil water sources has also been noted by Jackson et al. (1999), Stratton et al. (2000) and Querejeta et al. (2007), who found that drought-deciduous tree species tended to rely on deeper water sources than evergreen species in a Brazilian Cerrado savanna, in a Hawaiian dry tropical forest and in a tropical agroforest vegetation in northern Yucatan, respectively.

P. tomentosa, which produces leaves and flowers at the end of the dry season or at the early of the wet season after about 2–4 leafless weeks, had a phenology largely decoupled from current rainfall and may require a more constant and reliable water source than evergreen *G. subaequalis*, which produces leaves in the wet season or at the early of the dry season and may be able to modulate the timing of new leaf production according to water availability in the shallow soil (Jackson et al., 1999). Lack of

plasticity in depth of water uptake in *G. subaequalis* in response to changing environmental conditions does not necessarily indicate lower competitiveness, as it may reflect high tolerance for low resource environments. An alternative explanation is that large water stores in succulent trunks or roots might have decoupled leaf flushing from seasonal water availability in some of the drought-deciduous tree species (Goldstein et al., 1998; Chapotin et al., 2006), which illustrates the numerous combinations of plant traits that can combine to produce different water use strategies in the same dry tropical ecosystem (Borchert et al., 2004).

Ψ_{md} was less negative in *G. subaequalis* than in *P. tomentosa* (Fig. 6); this corresponds with results from Hawaiian dry tropical forests (Stratton et al., 2000), from seasonally dry neotropical forests (Jackson et al., 1995, 1999) and from semiarid pinyon-juniper woodland (Flanagan et al., 1992), that evergreen species had a less negative water potential than the deciduous. *G. subaequalis*, which had a relatively high Ψ_{md} , exhibited an ability to expand and maintain leaves nearly continuously. This apparent anomaly may be partially explained by the spatial distribution of *G. subaequalis*. Individuals of *G. subaequalis* were consistently located at least four times further from other individuals than the remaining species (Liu, personal observation), a distribution that may facilitate access to a larger soil volume with a higher water content in the absence of competition from neighboring individuals (Stratton et al., 2000). Meinzer et al. (1999) pointed out that the extensive horizontal area explored by roots systems 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. In addition, species relying primarily on shallow soil water are relatively drought tolerant and therefore able to sustain growth during periods of low soil water availability, whereas species tapping deeper sources of soil water appear to behave as drought avoiders, and tend to drop their foliage and exercise strong stomatal control of transpiration during the dry season (Stratton et al., 2000).

4.2. Use of fog water by plants

Soil surficial recharge from rain was quite sparse during the 2005 dry season (about 70% lower than the mean; Fig. 2), and fog water dripping may be the only source of water inputs during this period. Nearly every morning during the dry season, especially during the foggy season (Fig. 1B) the wetness inside the forest was similar to a light rain. The tree leaves were covered by water drops and within the forest floor there were many fog-wetted soil patches owing to the 'dripping point' effect (Bruijnzeel, 2001). Consequently, annual fog water dripping amount for this year reached to 103.2 mm, higher than the mean (89.4 mm).

During the dry season, the about 2-year-old *P. tomentosa* seedlings exhibited mean $\delta^{18}\text{O}$ values closer to the values of the shallowest soil layer and more enriched than values in the other soil layers, suggesting that seedlings obtained water from about 5 cm depth in the soil profile (Fig. 4). This is quite consistent with the visual inspection during our seedling sampling that seedling roots of this species were mainly restricted to the upper 8 cm of the soil. Output from the mixing model also indicated that the percentage of water used by seedlings from fog water dripping was around 23–59%, demonstrating that water from fog water dripping in the shallower soil horizons was an important source for seedling growth during the dry season, especially at the peak of the dry season (Fig. 5). This is likely because seedling root biomass was greatest in shallow horizons where uptake of fog water would be most efficient, as previously shown by Corbin et al. (2005). A decreased fog water uptake during the early of the dry season appeared to be related to the better soil water conditions (Fig. 3). A previous study on this site

(Liu et al., 2005) also pointed out that the shallower soil water, which had isotopic compositions usually between those of the rain and fog water dripping, was a mixture of the two waters, with more fog water contained in the late of the dry season than in the early of the dry season. Consistent with the long drought spell in the dry season, Ψ_{md} of *P. tomentosa* seedling was significantly lower at the peak of the dry season than at the early of the dry season (Fig. 6). The lack of a more substantial difference in Ψ_{md} between seedlings and trees at the early of the dry season may be due to sampling in December, which was still early in the seasonal surface dry-down cycle, with a 29 mm pulse of rain 12 days previous to the sampling date (Fig. 2). Similarly, Flanagan et al. (1992) and Donovan and Ehleringer (1994) also noted that plant water potential was more negative in species relying on uptake of precipitation near the soil surface than in species with access to deep soil water. However, in an earlier study of differential utilization of summer rains by desert plants it was observed that higher plant water potentials were correlated with greater reliance on summer precipitation as a water source (Ehleringer et al., 1991).

Dawson (1998) hypothesized that smaller trees and understory species using more fog water than larger trees is consistent with rooting depth information since smaller trees possess a greater fraction of shallow roots and may therefore use a greater proportion of shallow soil water that is from fog water dripping. Our results tend to support this hypothesis. Similarly, Corbin et al. (2005) found that the most likely zone of active water use from fog in summer drought was at approximately 10 cm depth, where plants could take advantage of the frequent moisture inputs from fog. Results from Weltzin and McPherson (1997), working in temperate savanna, Williams and Ehleringer (2000), in pinyon-juniper forests, and Donovan and Ehleringer (1994) in shrub community, that plants/seedlings relied on shallower root water uptake where precipitation was relatively predictable, are also consistent with our findings. However, it must be pointed out that direct fog water uptake through foliage may be important although it is likely a much smaller fraction than that taken up through roots (Dawson, 1998; Burgess and Dawson, 2004), but the uptake was not quantified in our study. In addition, fog water use by the mature trees through roots was not considered because mature tree roots were restricted to mainly below 15 cm depth of the soil profile. Hence, our estimates of fog water use by plants may be conservative, in that they only examine direct fog water use via root uptake and not other effects (such as foliar uptake of fog water or reduced transpiration), as previously pointed out by Dawson (1998).

4.3. Implications

Availability of water has frequently been shown to influence species' distribution in many ecosystems (Ehleringer et al., 2000; Corbin et al., 2005; Goldstein et al., 2008), and it has been suggested that the distribution of certain vegetation types rely on 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. It has been suggested that intercepted fog water which remains on foliage may be considered as a net gain, since the energy expended in its evaporation from the leaf surfaces would have been used in transpiration of an equal amount of water from the soil (Bruijnzeel, 2001). Reduction of evapotranspiration through reduction of the number of hours of sunshine and the day/night time temperature were also considered important if it takes place during periods when plants are especially water stressed (Dawson, 1998; Burgess and Dawson, 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 studied 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. They also pointed out that fog has indirect effects on the rate of tree photosynthesis and respiration as the aerial environment is greatly altered in terms of vapour pressure deficit, radiation and temperature. Furthermore, it is worth noting that frequent wetting and direct uptake of water by canopy elements may have consequences for cambial development and could result in complex patterns of xylem development and branch hydraulic resistances (Burgess and Dawson, 2004).

Our results suggest that the about 2-year-old *P. tomentosa* seedlings obtained water from about 5 cm depth of the soil profile, with Ψ_{md} values significantly lower at the peak of the dry season than at the early of the dry season. This indicates that seedlings suffered greater water stress and greatly relied on available moisture from fog water, although it could not completely meet plant's water use. The ability to take up a greater proportion of shallower/upper soil water that is mostly from fog water dripping during the pronounced dry season, is likely the key feature allowing *P. tomentosa* seedlings to thrive through the long drought spell. Previous study on seed germination and seedling growth in this forest site (Yu et al., 2008) showed that *P. tomentosa* had lower dehydration tolerance and seeds appeared to germinate anywhere in the forest, with high germination rate and germination percentage. This strategy enhanced the probability of successful regeneration for this species. Moreover, both morphological and physiological traits showed that although seedlings of *P. tomentosa* were deep-shade-tolerant in the forest understory, they grew better in small forest gaps, where there was more fog water dripping owing to 'dripping points' effect (Bruijnzeel, 2001) and higher diffuse radiation (Yu et al., 2008). Thus, Yu et al. proposed that the ability for *P. tomentosa* seeds to germinate and for its seedlings to grow in the forest understory might explain why it is one of dominant canopy species in the SE Asian tropical rainforests.

Clearly, seedlings of *P. tomentosa* were able to adjust the allocation of resources and thus to acclimate to the spatiotemporal microenvironment changes in the tropical rainforest. As mentioned above, seedlings of *P. tomentosa* greatly relied on available fog water at the peak of the dry season compared to the early of the dry season, suggesting that seedlings may encounter greater water stress during a drier-than-average dry season/year (such as that in 2005) compared to average or wet years. In consistent with this expectation, earlier observation indicated that during the dry season of 2003 (30.5 mm, about 81% lower than the mean), some species seedlings (such as *P. tomentosa*, *G. subaequalis* and *T. myriocarpa*) in this forest showed considerable water stress, with some being wilting or even died (Zhou, personal communication). Earlier study also pointed out that higher fog water dripping during dry years implies that fog water is more important in sustaining this type of rainforest vegetations 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 their redwood forest site in California. Since both seedlings and shallow-rooted understory species require moisture and cool conditions to regenerate (Feng et al., 2004; Cai et al., 2009), it might be expected that some other tree seedlings and understory species also partially rely on fog moisture in the seasonal rainforest during the dry season. But further research is needed.

Acknowledgements

The authors are very grateful to the two anonymous reviewers for providing constructive comments that greatly improved this manuscript. We thank the staff of the Xishuangbanna Station for

Tropical Rainforest Ecosystem Studies. Special thanks also go to Liu M.N., Zhou Z.H. and Shi M. for their field assistance. We greatly appreciate the financial supports from the National Science Foundation in China (30770368 and 30770385), and the "Western Light Program" of the Chinese Academy of Sciences.

References

- Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* 19, 282–289.
- Bonal, D., Atger, C., Barigah, T.S., Ferhi, A., Guehl, J., Ferry, B., 2000. Water acquisition patterns of two wet tropical canopy tree species of French Guiana as inferred from $H_2^{18}O$ extraction profiles. *Annals of Forest Science* 57, 717–724.
- Borchert, R., Meyer, S.A., Felger, R.S., Porter-Bolland, L., 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13, 409–425.
- Bruijnzeel, L.A., 2001. Hydrology of tropical montane cloud forest: a reassessment. *Land Use and Water Resources Research* 1, 1–18.
- Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell and Environment* 27, 1023–1034.
- Cai, Z.Q., Schnitzer, S.A., Bongers, F., 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161, 25–33.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595.
- Cao, M., Zhang, J.H., Feng, Z.L., Deng, J.W., Deng, X.B., 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, SW China. *Tropical Ecology* 37, 183–192.
- Chapotin, S.M., Razanameharizaka, J.H., Holbrook, N.M., 2006. Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytologist* 169, 549–559.
- Corbin, J.D., Thomsen, M.A., Dawson, T.E., D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. *Oecologia* 145, 511–521.
- Darrouzet-Nardi, A., D'Antonio, C.M., Dawson, T.E., 2006. Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow. *Plant and Soil* 285, 31–43.
- Dawson, T.E., 1998. Fog in the redwood forest: ecosystem inputs and use by plants. *Oecologia* 117, 476–485.
- Dawson, T.E., Mambelli, S., Plamboeck, A.H., Tempter, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33, 507–559.
- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and wood plant in a shortgrass steppe community. *Oecologia* 117, 504–512.
- Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8, 287–297.
- Drake, P.L., Franks, P.J., 2003. Water resource partitioning, stem xylem hydraulic properties, and plant water use strategies in a seasonally dry riparian tropical rainforest. *Oecologia* 137, 321–329.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.F.S., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88, 430–434.
- Ehleringer, J.R., Roden, J., Dawson, T.E., 2000. Assessing ecosystem-level water relations through stable isotope ratio analysis. In: Sala, O.E., Jackson, R.B., Mooney, H.A. (Eds.), *Methods in Ecosystem Science*. Academic Press, San Diego, pp. 181–198.
- Ewe, S.M.L., Sternberg, L.S.L., 2002. Seasonal water-use by the invasive exotic, *Schinus terebinthifolius*, in native and disturbed communities. *Oecologia* 133, 441–448.
- Feng, Y.L., Cao, K.F., Feng, Z.L., 2004. Photosynthetic characteristics, dark respiration and specific leaf weight in seedlings of four tropical tree species under three different light regimes. *Photosynthetica* 42, 431–437.
- Field, T.S., Dawson, T.E., 1998. Water sources used by *Didmopanax pittieri* at different life stages in a tropical cloud forest. *Ecology* 79, 1448–1452.
- Flanagan, L.B., Ehleringer, J.R., Marshall, J.D., 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment* 15, 831–836.
- Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavelier, J., Jackson, P.C., Celis, A., 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell and Environment* 21, 397–406.
- Goldstein, G., Meinzer, F.C., Bucci, S.J., Scholz, F.G., Franco, A.C., Hoffmann, W.A., 2008. Water economy of Neotropical savanna trees: six paradigms revisited. *Tree physiology* 28, 395–404.
- Hutley, L.B., Doley, D., Yeyes, D.J., Boonsaner, A., 1997. Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog. *Australian Journal of Botany* 45, 311–329.
- Ingraham, N.L., Matthews, R.A., 1995. The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. *Journal of Hydrology* 164, 269–285.
- Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M., 1995. Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101, 197–203.

- Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.W., Caldas, L., 1999. Partitioning of soil among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology* 19, 717–724.
- Lin, G.H., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Coorido Plateau. *Oecologia* 106, 8–17.
- Liu, W.J., Meng, F.R., Zhang, Y.P., Liu, Y.H., Li, H.M., 2004. Water input from fog drip in the tropical seasonal rainforest of Xishuangbanna, SW China. *Journal of Tropical Ecology* 20, 517–524.
- Liu, W.J., Zhang, Y.P., Li, H.M., Liu, Y.H., 2005. Fog drip and its relation to ground-water in the tropical seasonal rainforest of Xishuangbanna, SW China: a preliminary study. *Water Research* 39, 787–794.
- Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, M.N., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121, 293–301.
- Moreira, M.Z., Sternberg, L.S.L., Nepstad, D.C., 2000. Vertical patterns of soil water uptake by plants in a primary forest and an abandoned pasture in the eastern Amazon: an isotopic approach. *Plant and Soil* 222, 95–107.
- Muthukumar, T., Sha, L.Q., Yang, X.D., Cao, M., Tang, J.W., Zheng, Z., 2003. Distribution of roots and arbuscular mycorrhizal associations in tropical forest types of Xishuangbanna, southwest China. *Applied Soil Ecology* 22, 241–253.
- Nippert, J.B., Knapp, A.K., 2007. Linking water uptake with rooting patterns in grassland species. *Oecologia* 153, 261–272.
- Pate, J.S., Dawson, T.E., 1999. Assessing the performance of woody plants in uptake and utilization of carbon, water and nutrients: implications for designing agricultural mimic systems. *Agroforestry Systems* 45, 245–275.
- Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127, 171–179.
- Querejeta, J.I., Estrada-Medina, H., Allen, M.F., Jimenez-Osornio, J.J., 2007. Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia* 152, 26–36.
- Ritter, A., Regalado, C.M., Aschan, G., 2009. Fog reduces transpiration in tree species of the Canarian relict heath-laurel cloud forest. *Tree Physiology* 29, 517–528.
- Romero-Saltos, H., Sternberg, L.S.L., Moreira, M.Z., Nepstad, D.C., 2005. Rainfall exclusion in an eastern Amazonian forest alters soil water movement and depth of water uptake. *American Journal of Botany* 92, 443–455.
- Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166, 262–276.
- Snyder, K.A., Williams, D.G., 2003. Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). *Functional Ecology* 17, 363–374.
- Sternberg, L.S.L., Swart, P.K., 1987. Utilization of freshwater and ocean water by coastal plants of southern Florida. *Ecology* 68, 1898–1905.
- Stratton, L.C., Goldstein, G., Meinzer, F.C., 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia* 124, 309–317.
- Thorburn, P.J., Hutton, T.J., Walker, G.R., 1993. Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forest. *Journal of Hydrology* 150, 563–587.
- Weltzin, J.F., McPherson, G.R., 1997. Spatial and temporal soil moisture partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* 112, 156–164.
- White, J.W.C., Cook, E.R., Lawrence, J.R., Broecker, W.S., 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. *Geochimica et Cosmochimica Acta* 49, 237–246.
- Williams, D.G., Ehleringer, J.R., 2000. Intra- and inter-specific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs* 70, 517–537.
- Yu, Y., Baskin, J.M., Baskin, C.C., Tang, Y., Cao, M., 2008. Ecology of seed germination of eight non-pioneer tree species from a tropical seasonal rain forest in SW China. *Plant Ecology* 197, 1–16.