

Is fog an important water source for woody plants in an Asian tropical karst forest during the dry season?

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ABSTRACT

Fog is an important supplemental source of water in regions with heavy fog and little rainfall. In the present study, we used the stable isotope content of xylem water to investigate the dry season water source partition between soil and fog water of two evergreen tree species (*Cleistanthus sumatranus* and *Lasiococca comberi*), two deciduous tree species (*Mayodendron igneum* and *Lagerstroemia tomentosa*), two liana species (*Acacia pennata* and *Combretum latifolium*) and understory seedlings of three tree species (*C. sumatranus*, *L. comberi* and *Celtis philippensis*) in a tropical karst forest in southern Yunnan, China. The soil gravimetric water content (GWC) and volumetric water content (VWC), pre-dawn leaf water potential ($\Psi_{\text{pre-dawn}}$) and leaf water absorbance were also measured. There were no significant differences in both GWC and VWC among 10 to 100 cm depths in the dry season. In the dry season 2009, $\Psi_{\text{pre-dawn}}$ of the two evergreen tree species and the understory seedlings down to -4.5 to -6.3 MPa, and which were significantly lower than those of a normal dry season. The proportion that fog contributed to xylem water ranged from 15.8% (understory seedling of *C. sumatranus*) to 41.3% (liana species *C. latifolium*). After immersing in water for 3 h, leaves of all the studied species absorbed a significant volume of water. Our results reveal that the woody plants in the tropical karst forest of Xishuangbanna use fog water as an important supplement in the dry season, with more fog water being used by lianas than by trees. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS foliar water uptake; tropical karst forest; lianas; dry season; stable isotopes

Received 31 March 2015; Revised 31 August 2015; Accepted 9 October 2015

INTRODUCTION

Fog plays an important role in the plant water relations and the hydrology of forest ecosystems in various regions of the world where fog is frequent. The occurrence of heavy fog in tropical montane cloud forests is a common phenomenon and is very important for the water balance of the forest ecosystems (Bruijnzeel, 2011; Goldsmith *et al.*, 2013). Fog may affect the water balance of forest ecosystems in three different ways. Firstly, fog may decrease the transpiration of plants (Limm *et al.*, 2009; Goldsmith *et al.*, 2013; Alvarado-Barrientos *et al.*, 2014). Secondly, fog can increase the soil water content by the drip of fog water intercepted by the canopy (Dawson, 1998; Liu *et al.*, 2005). Thirdly, some plants can directly absorb water through their leaves [foliar water uptake (FWU)] (Burgess and Dawson, 2004; Simonin *et al.*, 2009;

Eller *et al.*, 2013; Goldsmith *et al.*, 2013). Limm *et al.* (2009) found that 80% of the dominant species in a redwood forest in coastal California exhibit a FWU strategy. Leaf cuticles (Yates and Hutley, 1995; Eller *et al.*, 2013), trichomes (Franke, 1967) and hydathodes (Martin and Willert, 2008) have been found to be involved in FWU. Ishii *et al.* (2014) demonstrated that the water uptake by leaves can also be stored internally. The fog water can alleviate the water stress of the plant, especially in the dry season (Dawson, 1998; Simonin *et al.*, 2009; Eller *et al.*, 2013; Gotsch *et al.* 2014, Liu *et al.*, 2014). Fog water contributes 13–45% of the annual transpiration by the coastal forests in California and may be even more important in dry year (Dawson, 1998). In the Atlantic forest of Brazil Eller *et al.* (2013) found that FWU contribute more than 26% of daily transpiration and enhanced the leaf water potential, leaf gas exchange and growth of *Drimys brasiliensis*, a key species of cloudy forests in the region.

Different functional groups of plants or plants in different developmental stages may have a different capacity for using fog water. Fog water tends to be more

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important for understory seedlings than for deeply rooted adult plants (Dawson, 1998; Liu *et al.*, 2010; Liu *et al.*, 2014). Liana abundance increases with the increase of seasonality and decrease of precipitation in seasonal tropical forest (Schnitzer *et al.*, 2005). Lianas have been found to have water use advantage over trees in dry season in tropical seasonal forests because they process well-developed roots that can access deeper soil water than the co-occurring trees (Chen *et al.* 2015). In the dry season, deciduous trees shed their leaves to avoid transpiration, while the evergreen trees maintain their water use to support their transpiration. Thus, evergreen trees may have a greater capacity for using the fog water to support the transpiration of their leaves. By using the stable isotope method it is possible to distinguish the dominant water sources of plants used by different functional groups (Dawson, 1998; Ehleringer and Dawson, 1992; Jackson *et al.*, 1999; Querejeta *et al.*, 2006; Liu *et al.*, 2010). In the present study, we will compare the fog water use capacity of plants from different functional groups in a tropical karst forest in SW China.

Karst habitats account for 10–15% of the world land and 14% of the land of China, with a particularly extensive distribution in SW China (Yuan, 1991; Ford and Willams, 2007). Karst forests are also rich in plant diversity, with many endemic species (Zhu *et al.*, 2003; Clements *et al.*, 2006). Because there are many fissures and holes and little soil overlying the limestone bedrock, plants in the karst areas can hardly access deep groundwater; thus, plants mostly use the water present in the shallow soil and the underlying bedrock crevice (Querejeta *et al.*, 2006; Querejeta *et al.*, 2007; Schwinning, 2008). Because of its location to the Asian monsoons belt, most of the rainfall in SW China occurs in a distinct rainy season with little rainfall in the dry season. The plants in karst habitats experience water stress frequently, especially in the dry season. In Xishuangbanna (Yunnan, SW China), heavy fog in the dry season plays a very important role in the water relations of plants and the hydrology of the tropical forest in this region (Cao and Zhang, 1997; Liu *et al.*, 2004; Liu *et al.*, 2014). Liu *et al.* (2014) found that both evergreen trees and understory seedlings in the karst forest of Xishuangbanna used significant amount of fog water as their primary water sources in the dry season. However, there is still a lack of information on the fog water use by other functional groups, notably lianas and deciduous trees.

In the present study, we compared dry season water source partition between soil and fog water of lianas, evergreen trees, deciduous trees and understory seedlings in the Xishuangbanna karst forest. We hypothesized that fog water played an important role in the dry season for tropical karst forest plants; specifically, lianas would depend more on soil water than trees with deeper roots,

while evergreen trees would use more fog water than deciduous trees to support their dry season water use.

MATERIALS AND METHODS

Study site and species

The present study site was located in a tropical karst forest ~3 km from Xishuangbanna Tropical Botanical Garden (XTBG) (21°55'39"N, 101°15'46"E, 700 m above sea level), in southern Yunnan, China. The present study site is very close to our previous study (Liu *et al.* 2014). However, the present study site was at a foot slope site with a much deeper soil (~100 cm), and the study site of Liu *et al.* (2013) was on a hill top with shallower soil depth (<40 cm). The mean annual temperature is 21.7 °C with the monthly mean temperature being 15.9 °C during the coldest month (December) and 25.7 °C during the warmest month (June). Because of the influence of the Asian monsoon, there is a distinct dry season from November to April. The annual rainfall is approximately 1500 mm with more than 80% occurring in the rainy season (Figure 1a). Between November and March there is heavy radiation fog from midnight (23:00–02:00) until mid-morning (09:00–11:00) (Liu *et al.*, 2004), with fog occurrence at least 20 days per month (Figure 1a). According to the climate data from a nearby weather station, rainfall in the severe dry season of 2009 was significantly less than normal (Figure 1b). The total amount of rainfall in the 3 months from December 2008 to February 2009 was 11 mm, or only one sixth of the long-term average value (65 mm; Figure 1a, b).

The soil at the study site is a brown calcareous and stony soil with pH of 7.3 (Zhang, 2006). The present study site is located on the western foot slope of a karstic hill. The soil here is deeper (~1.0 m) compared with that of the top of the hill. The forest is dominated by *Cleistanthus sumatranus* (Miquel) Müller Argoviensis, *Lasiococca comberi* Haines, *Celtis philippensis* Blanco, *Lagerstroemia tomentosa* C. Pres, *Tetrameles nudiflora* R. Brown and *Garuga pinnata* Roxburgh (Zhu *et al.*, 2003). There are abundant lianas, with *Combretum latifolium* Blume and *Acacia pennata* (Linnaeus) Willdenow being the two most common species.

Two evergreen tree species (*C. sumatranus* and *L. comberi*), two deciduous tree species (*Mayodendron igneum* and *L. tomentosa*) and two liana species (*C. latifolium* and *A. pennata*) were selected for this study. Understory seedlings of three tree species (*C. sumatranus*, *L. comberi* and *Celtis philippensis*) were also chosen. The diameter at breast height (DBH) of the tree species ranged from 22.6 cm (*M. igneum*) to 47.7 cm (*L. tomentosa*). The DBH of the lianas ranged from 6.5 cm (*C. latifolium*) to 10.2 cm (*A. pennata*). The height of the understory seedlings was 60–80 cm. Both liana species are deciduous, which shed

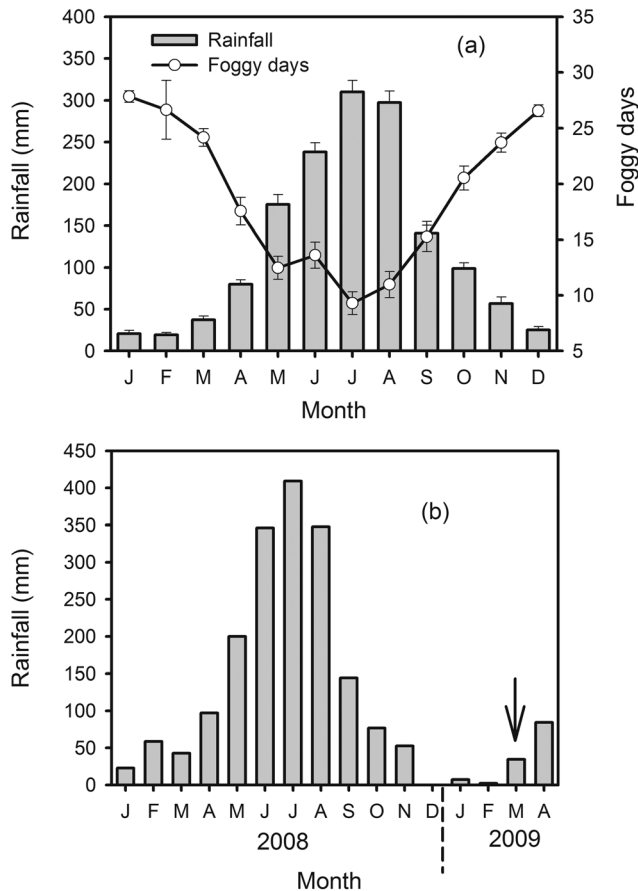


Figure 1. Average monthly rainfall (during 1959–2009) and number of foggy days (during 1975–2009) at an ecological station near the present study site (a) plus the monthly rainfall from January 2008 to April 2009 (b). The down ward arrow in (b) indicates the sampling date (i.e. from 13 to 19 March 2009).

their leaves in the middle of the dry season (January to February) and flush new leaves at the end of March. The deciduous trees *L. tomentosa* and *M. igneum* shed their leaves in February and flush leaves in late March.

Leaf water potential

The pre-dawn leaf water potentials of the two evergreen tree species and the seedlings were measured in the early morning (6:00–8:00) at the peak of the dry season (March 2009) and in a normal dry season (March 2015) using a pressure chamber (PMS, Corvallis, OR, USA). Sun-lit leaves were sampled and immediately put into plastic bags with wet tissues and taken to the nearby laboratory. Two leaves or twigs from 4 to 6 individuals for each species were sampled. The pressure measurements were completed within 1 h after harvesting.

Rain water, fog water, plant and soil sampling

Eight rain water samples were collected during the year 2008 (three samples from September, three samples from

October and two samples from November). There were no significant rain in December 2008, January and February 2009 and the beginning of March. Samples of rainwater were collected immediately from a rain gauge after rain ceased or in the early morning when rain fell overnight. The sampling dates for fog water, soil water and wood samples were from 13 to 19 March 2009. The fog water was collected from a steel frame placed in the open field of XTBG during 3 days with heavy fog in the early morning at the peak of the dry season (March 2009). Both rainwater and fog water were then transferred into small glass bottles with the lid closed tightly and wrapped with parafilm and kept in a refrigerator at a temperature of 4 °C. The isotopic composition of the fog water collected in the present study fell within the range of values determined for dry season canopy drip in the same region (Liu *et al.* 2005; 2014).

Both soil and wood samples were collected in the early morning to minimize evaporation. The soil depth was 100 cm, with heterogeneously fractured limestone bedrock below. Four pits of ~1 m diameter were dug. Soil samples were taken from soil pit sidewalls immediately after excavation for gravimetric water content (GWC) measurement and isotope analysis. Soil samples of ~20 g were collected at depth of 10, 30, 50, 70, 90 and 100 cm for GWC measurement, while soil samples of ~2 g were taken at depth of 10, 50, and 100 cm for isotopic analysis. For each depth, one soil sample was collected at ~3 cm deep (horizontally) into the sidewalls of pits to avoid alteration of water isotopic composition by evaporative enrichment during the process of excavation. Soil samples for isotope measurement were kept in a refrigerator at a temperature of –20 °C until analysis. The fresh weight of a soil sample (W_{fresh}) was determined then it was dried in an oven at 105 °C for 24 h to obtain the dry weight (W_{dry}). The GWC was calculated as $\text{GWC} = (W_{\text{fresh}} - W_{\text{dry}}) / W_{\text{dry}}$. The soil bulk densities from 10 to 100 cm were measured from three different positions within the study site. The soil volumetric water content (VWC) was calculated by multiplying the GWC by soil bulk density at different depths.

Both for adults and seedlings four individuals of each species were chosen for xylem water sampling. For the adult plants, wood samples (~2 g of each) were collected using an increment borer at the height of 1.3 m. For the understory seedlings, wood samples were obtained from the stem segments by harvesting the seedlings. All green tissues were removed from the stem to avoid contamination of xylem water by isotopically enriched water (Ehleringer and Dawson 1992). The wood samples were put into glass bottles immediately, and the bottles were closed and wrapped with parafilm. The wood samples were then put into a cooler and taken to the laboratory immediately.

The wood samples were also stored in a refrigerator at a temperature of –20 °C. Water was extracted from the soil

and wood samples using a cryogenic vacuum distillation line (Ehleringer *et al.*, 2000). The $\delta^{18}\text{O}$ and δD of the rainwater, fog water, soil water and xylem water were measured using an isotope ratio mass spectrometer (Thermo Finnigan, USA) at the Isotope Laboratory of the Chinese Academy of Forestry with accuracies of ± 1.5 and $\pm 0.2\text{‰}$ for δD and $\delta^{18}\text{O}$ respectively.

Foliar water uptake capacity measurement

The FWU capacity was measured at both the beginning of the dry season in December 2010 and the rainy season in 2015 following Limm *et al.* (2009). Before dusk, one to two leaves from each of 4 to 6 individuals were sampled and put into plastic bags with wet tissues inside. The samples were taken to the laboratory immediately where the leaf fresh weight (W_1) and leaf area (A_{leaf}) were measured. The leaves were then immersed in water for 3 h. The petiole was wrapped with Parafilm and fixed above the water. The leaves were then dried with tissues to obtain the saturated weight (W_2). Any residual water present on the leaf surface after tissue-drying was corrected according to Limm *et al.* (2009). The surface-dry leaf was weighed (W_3) and submerged in water again for 1 s, after which the leaf was dried again and re-weight (W_4). The residual water on the leaf surface was calculated as the difference between W_4 and W_3 . Finally, the leaves were dried in an oven at 70°C for 24 h, and the dry weight (W_d) was determined. The leaf water uptake capacity (LWC) per leaf unit area was calculated as $\text{LWC} = [(W_2 - W_1) - (W_4 - W_3)] / A_{\text{leaf}}$, and the increase in leaf water content was calculated as plant water index = $\{[(W_2 - W_1) - (W_4 - W_3)] / (W_1 - W_d)\} * 100\%$.

Data analysis

We calculated the contribution of rain water and fog water to soil water at different depths in the dry season 2009 with isoerror1_04 (Phillips, 2001). Volume weighted $\delta^{18}\text{O}$ of rain water and the GWC weighted mean isotopic values for soil water were used for the calculation. We found that fog water only contributed 10% to the soil water above 10 cm depth, while nearly all the soil water ($>99\%$) above 50 cm depth was contributed by previous rainwater (Table S2). In the following calculation of water source partitions, fog water (foliar uptake) and soil water (root uptake) were taken as the dominant water sources for xylem water. The contribution to xylem water by different water sources, i.e. shallow soil (<50 cm), deep soil (50–100 cm) and fog water, was calculated with a three source model using ISOSOURCE (Phillips and Gregg, 2003). Because the isotope signatures of D and ^{18}O are closely correlated with each other ($r^2 = 0.91$, $P < 0.0001$), only $\delta^{18}\text{O}$ was used in the calculations. The differences in soil gravimetric and VWCs among different depths were analysed with one-way ANOVA in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). The differences in dry season

pre-dawn leaf water potential between 2009 and a regular dry season (2015) were analysed with the independent samples *t*-test in SPSS 16.0. The significance of water absorption and increase in leaf water content after immersion for 3 h was tested using the one-sample *t*-test in SPSS 16.0.

RESULTS

There were no significant differences for both soil GWC (with mean value 20.9%) and soil VWC (with mean value $27.9\text{ cm}^3\text{ H}_2\text{O cm}^{-3}\text{ soil}$) among different depths in the dry season 2009 (Figure 2a, b). The average soil bulk density is 1.33 g cm^{-3} and ranged from 1.27 g cm^{-3} at 10 cm depth to 1.37 g cm^{-3} at 50 cm depth (Table S1). The soil GWC decreased only slightly from the 10 cm depth ($21.3 \pm 0.3\%$) to the depth of 100 cm ($20.7 \pm 0.6\%$), while the VWC ranging from $26.8\text{ cm}^3\text{ H}_2\text{O cm}^{-3}\text{ soil}$ at 90 cm depth to

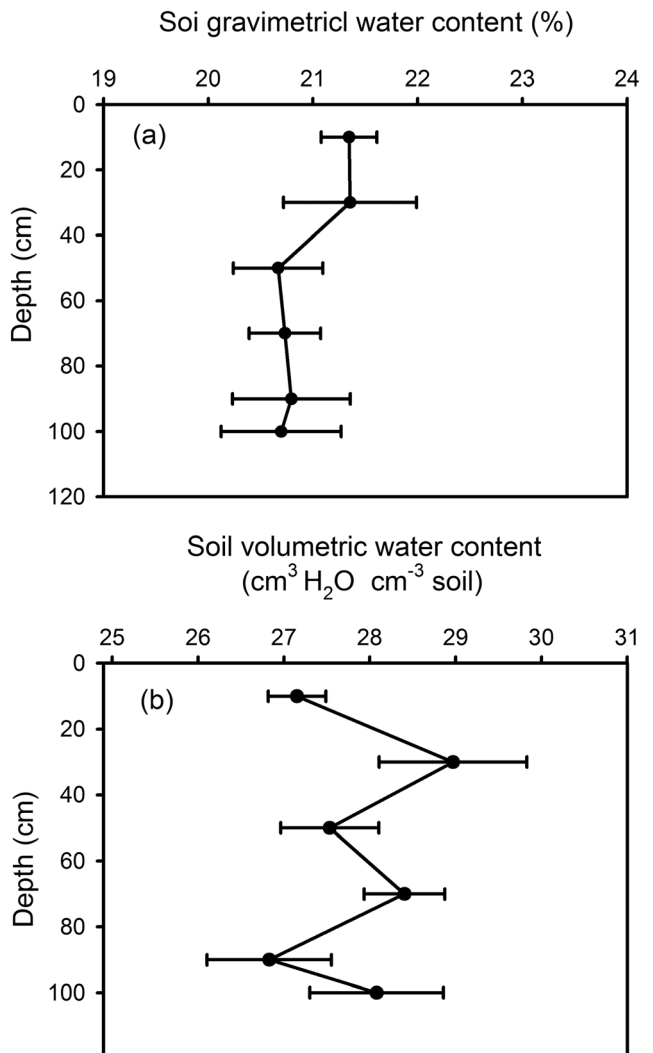


Figure 2. Gravimetric soil water content (means ± 1 SE; $n = 4$) (a) and volumetric soil water (b) at different depths in a tropical karst forest at the peak of dry season in March 2009.

29.0 cm³ H₂O cm⁻³ soil at 30 cm depth (Figure 2b). Plants in karst forest experienced severe water stress at the peak of the dry season in March 2009. The pre-dawn leaf water potentials ($\Psi_{\text{pre-dawn}}$) of the evergreen tree species and understory seedlings of three tree species during that time were significantly lower than those of dry season with a regular rainfall (Figure 3). The $\Psi_{\text{pre-dawn}}$ in the dry season of 2009 ranged from -4.50 ± 0.72 MPa (the adult evergreen of *Cleistanthus sumatranus*) to -6.28 ± 0.25 MPa (understory seedlings of *C. sumatranus*), while the $\Psi_{\text{pre-dawn}}$ in a normal dry season 2015 ranged from -0.78 ± 0.22 MPa (adult *Lasiococca comberi*) to -1.77 ± 0.15 MPa (seedlings of *C. sumatranus*). The isotope ratios of soil water at the 10 cm depth were significantly more enriched than those at 50 and 100 cm depths, but there was no significant difference in soil water isotopic ratios at 50 and 100 cm depths (one-way ANOVA, SPSS 16.0).

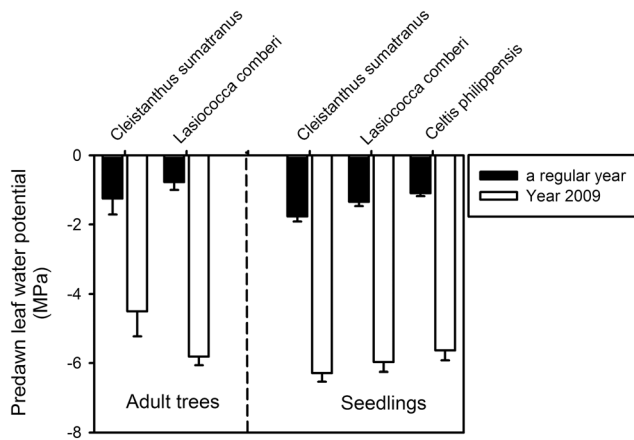


Figure 3. Pre-dawn leaf water potential ($\Psi_{\text{pre-dawn}}$) of the evergreen trees *Cleistanthus sumatranus* and *Lasiococca comberi*, as well as the understory seedlings *C. sumatranus*, *L. comberi* and *Celtis philippensis* at the peak of the dry season in March of a year with regular rainfall (closed bars) and 2009 (open bars). Values are means ± 1 SE ($n=4-5$).

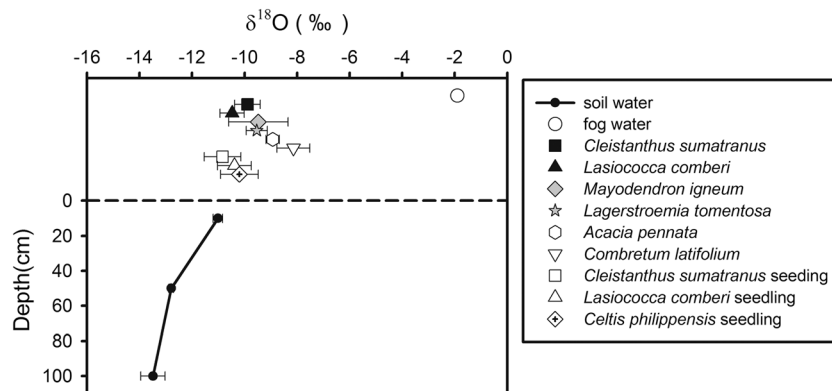


Figure 4. Isotopic composition ($\delta^{18}\text{O}$) of soil water (●) at 10, 50 and 100 cm depths, fog water (○), xylem water in two evergreen tree species *Cleistanthus sumatranus* (■) and *Lasiococca comberi* (▲), two deciduous tree species *Mayodendron igneum* (◆) and *Lagerstroemia tomentosa* (☆), two liana species *Combretum latifolium* (◇) and *Acacia pennata* (▽) and understory seedlings of three tree species, *Cleistanthus sumatranus* (□), *Lasiococca comberi* (△), and *Celtis philippensis* (◇). Values are means ± 1 SE. The fog water was collected during three days with heavy fog at the peak of dry season in March 2009. Wood samples were collected from four trees or seedlings for each species.

The isotopic ratios of fog water were consistently higher than those of rainwater, soil water and xylem water samples, with average $\delta^{18}\text{O}$ and δD values of -1.9 ± 0.2 and $24.4 \pm 2.4\text{‰}$ respectively (Figures 4 and 5a, b). The isotope ratios of rain water during 2008 ranged from -9.2 to -15‰ for $\delta^{18}\text{O}$ and from -45.7 to 105.7‰ for δD respectively (Figure 5a). The isotope ratios of soil water at different depths are distributed more close to rainwater than fog water. By calculating with a two-source mixing model with fog water and rain water as the source water for soil water, nearly all ($>99\%$) the shallow soil water (<50 cm) was contributed by rainwater, and less than 1% of shallow soil water was contributed by fog water drip. The $\delta^{18}\text{O}$ values of xylem water ranged from $-8.1 \pm 0.6\text{‰}$ in the liana *Combretum latifolium* to $-10.8 \pm 0.7\text{‰}$ in the understory seedlings of *C. sumatranus*, whereas δD values ranged from $-74.3 \pm 2.4\text{‰}$ in *C. latifolium* to $-93.0 \pm 4.2\text{‰}$ in the evergreen tree *L. comberi* respectively (Figures 4 and 5). The isotopic ratios of xylem water located to the right of the local meteoric water line indicate that plants utilized water sources that had been subjected to evaporative isotopic enrichment (Ehleringer *et al.* 2000, Liu *et al.* 2005). The xylem water of lianas had the most enriched isotopic values, and the understory seedlings had the least enriched ratios (Figures 4 and 5).

The xylem water isotopic ratios of all the studied plant species were closer to the average isotopic ratios of soil water than that of the fog water. The isotopic ratios of xylem water of the two lianas *Acacia pennata* and *C. latifolium* were closer to the isotopic ratios of fog water than the xylem water of other plants, while the isotopic ratios of the understory seedlings and evergreen tree *L. comberi* were closer to soil water signatures than the other plants (Figures 4 and 5). The two deciduous tree species *Lagerstroemia tomentosa* and *Mayodendron igneum* shared isotope ratios closer to those of fog water compared with that of the two evergreen trees (Figures 4 and 5). Based on the results

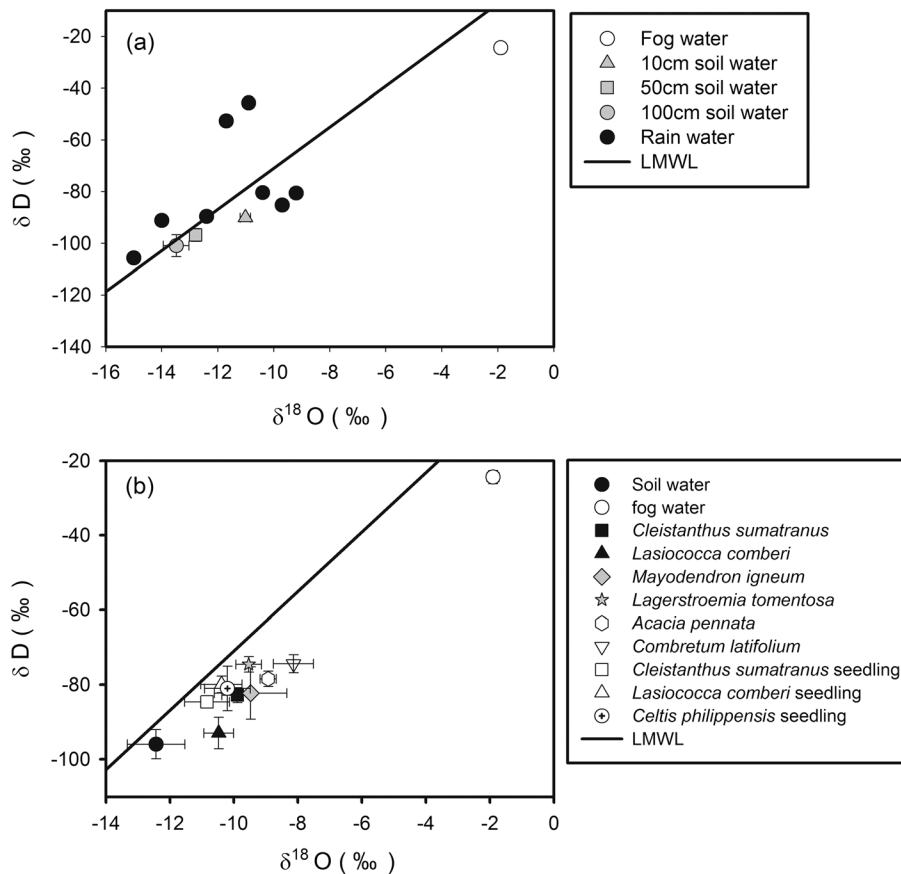


Figure 5. Scatterplot of the isotopic composition (δD and $\delta^{18}O$) of rainwater (closed circles) during August, September, October and November of 2008 and soil water in 10 cm (grey triangle), 50 cm (grey square), 100 cm (grey circle) and fog water (open circle) (a). Scatterplot of the isotopic composition (δD and $\delta^{18}O$) of the karst soil water (●), fog water (○), xylem water in two evergreen tree species *Cleistanthus sumatranus* (■) and *Lasiococca comberi* (▲), two deciduous tree species *Mayodendron igneum* (◇) and *Lagerstroemia tomentosa* (☆), two liana species *Combretum latifolium* (○) and *Acacia pennata* (▽) and understory seedlings of three tree species, *Cleistanthus sumatranus* (□), *Lasiococca comberi* (△), and *Celtis philippensis* (◇) (b). The straight line is the local meteoric water line [adapted from Liu *et al.* (2005)]. Soil water in Figure 5b represents the average values for three different depths (10, 50 and 100 cm). The fog water was collected during three days with heavy fog at the peak of the dry season in March 2009. Wood samples were collected from four trees or seedlings of each species. Crossed bars represent mean ± 1 SE.

obtained with the IsoSource mixing model (Phillips and Gregg, 2003), all the plant species in the present study used fog water as a source with the proportions ranging from 15.8% (the understory seedling of *C. sumatranus*) to 41.3% (liana species *C. latifolium*) (Table I). The two liana species used more fog water compared with the other species. The mean fog water proportions used by species *A. pennata* and *C. latifolium* were 33.7 and 41.3% respectively. Compared with the evergreen tree species, the two deciduous tree species also used more fog water. The proportion of fog water used by the understory seedlings ranged from 15.8% (*C. sumatranus*) to 21.4% (*Celtis philippensis*). There was a wide range of possible combinations of shallow soil water and deeper soil water.

The leaf water content of the six plant species examined significantly increased after being immersed in water for 3 h (Figure 6). The FWU capacity ranged from $0.64 \pm 0.12 \text{ mg H}_2\text{O cm}^{-2}$ for the deciduous species *M. igneum* to $1.02 \pm 0.14 \text{ mg H}_2\text{O cm}^{-2}$ for the liana *C. latifolium*. The

percent increase in leaf water content ranged from $4.5 \pm 0.7\%$ for *M. igneum* to $13.8 \pm 4.3\%$ for the evergreen tree *L. comberi*. In the rainy season, FWU capacity ranged from $0.14 \pm 0.04 \text{ mg H}_2\text{O cm}^{-2}$ for the evergreen tree *L. comberi* to $0.70 \pm 0.13 \text{ mg H}_2\text{O cm}^{-2}$ for the deciduous tree *M. igneum* (Figure S1), and all the species except deciduous tree *M. igneum* and liana *A. pennata* had significantly lower leaf absorbance than those of dry season (Independent samples *t*-test).

DISCUSSION

Fog as an important water source for the woody plants in tropical karst forest

Our results showed that fog water accounted for an important proportion of the xylem water in all the woody plants examined, ranging from 15.8% in the understory seedlings of *Cleistanthus sumatranus* to 41.3% in the liana species *Combretum latifolium*. In a karst forest close to the

Table I. The proportions of water sources inferred for different plant species in a tropical karst forest at the peak of the dry season in March 2009 using fog water, shallow soil water (<50 cm) and deep soil water (50–100 cm) as potential sources of plant xylem water with a single isotopic signature ($\delta^{18}\text{O}$) (Phillips and Gregg 2003).

Species	Functional group	Fog	Shallow soil water % (<50 cm)	Deep soil water % (50–100 cm)
<i>Cleistanthus sumatranus</i>	Evergreen tree	24.3 (19–39)	40.2 (0–81)	35.5 (0–72)
<i>Lasiococca comberi</i>	Evergreen tree	18.6 (13–24)	43.2 (0–87)	38.2 (0–77)
<i>Mayodendron igneum</i>	Deciduous tree	28 (23–33)	38.4 (0–77)	33.6 (0–68)
<i>Lagerstroemia tomentosa</i>	Deciduous tree	28 (23–33)	38.4 (0–77)	33.6 (0–68)
<i>Acacia pennata</i>	Liana	33.7 (29–38)	35.2 (0–71)	31.1 (0–63)
<i>Combretum latifolium</i>	Liana	41.3 (37–45)	31 (0–63)	37.7 (0–56)
<i>Cleistanthus sumatranus</i>	Seedling	15.8 (10–21)	44.5 (0–90)	39.7 (0–80)
<i>Lasiococca comberi</i>	Seedling	19.5 (14–25)	42.7 (0–86)	37.7 (0–76)
<i>Celtis philippensis</i>	Seedling	21.4 (16–26)	41.6 (0–84)	37 (0–75)

The mean values with the range of minimum/maximum proportions (in parentheses) were also given.

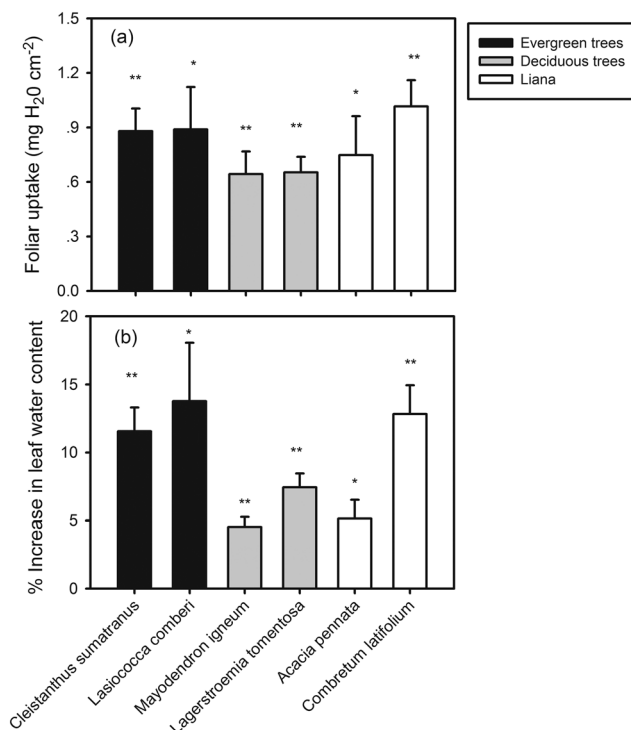


Figure 6. The dry season foliar water uptake (a) and percent increase in leaf water content (b) after immersing leaves in water for 3 h. The plant species are the evergreen trees (black bars) *Cleistanthus sumatranus* and *Lasiococca comberi*, the deciduous tree species (grey bars) *Mayodendron igneum* and *Lagerstroemia tomentosa* and the liana species (open bars) *Combretum latifolium* and *Acacia pennata*. The asterisk indicates the foliage absorb water significantly more than 0 mg H₂O cm⁻² (a) and significantly increased in leaf water content (b) (one sample t-test, * $P < 0.05$, ** $P < 0.01$).

present sampling site, Liu *et al.* (2014) found that fog water contributed 3.1 to 7.2% of the water source used by adult tree species in the dry season versus 23.8% for understory seedlings. The contributions of fog water as a source to adult trees found by the present study are higher compared with those the previous studies (Dawson, 1998; Liu *et al.*, 2014). This could be the consequence of the severe water

stress developed in the prolonged dry season 2009 at Xishuangbanna. The total rainfall from 7 November 2008 to 26 March 2009 was only 11.6 mm (Figure 1b), which was only one sixth of the long-term average value (65 mm). The pre-dawn leaf water potentials measured in the present study were also much lower than those for a normal dry season (Figure 3) and were as negative as those observed in 2010, when there was another severe drought across SW China (Stone, 2010; Huang *et al.*, 2013). Our results thus indicate that the contribution of fog water may well be more important for plant water relations during severe drought conditions in tropical karst forest. The present study further confirms the importance of fog water to plants in karst habitats (cf. Liu *et al.* 2014).

However, there was a wide range of possible combinations of contributions by shallow soil water and deeper soil water, and the model used failed to distinguish between the contributions by shallow and deeper soil water (Table I). The soil water was mainly contributed by the previous rainwater. In the presently study, nearly all the shallow soil water (<50 cm) was contributed by rainwater, and less than 1% of shallow soil water was contributed by fog water drip. However, Liu *et al.* (2005) found that the contribution of fog water to shallow soil water is considerable higher in a nearby non-karst forest locating in a valley and having much denser canopy comparing to this study.

Foliar water uptake

Our study indicated that foliar absorption playing an important role in the dry season water use for plants in tropical karst forest. Leaves of all the plant species examined in the present study had the potential to absorb fog water. After immersing in water for 3 h, leaves of all the plant species had taken up significant amount of water (Figure 5). Foliar water uptake (FWU) is a common phenomenon, which may ease plant water stress and improve plant photosynthetic performance and growth in a variety of ecosystem (Burgess and Dawson, 2004; Limm *et al.*, 2009;

Simonin *et al.*, 2009; Eller *et al.*, 2013; Goldsmith *et al.*, 2013; Gotsch *et al.* 2014). Previous studies have suggested that the absorbed fog water can be transported to the belowground parts of the plants and even moisten the soil close to the roots (Burgess and Dawson, 2004; Eller *et al.*, 2013; Goldsmith *et al.*, 2013). Leaf cuticles (Yates and Hutley, 1995; Eller *et al.*, 2013), trichomes (Franke, 1967), hydathodes (Martin and Willert, 2008), polysaccharides, pectin and mucilage plugs (Westhoff *et al.*, 2009; Eller *et al.*, 2013) have been found to be involved in FWU. However, the specific pathways and mechanisms of FWU in water deficient conditions still need further study. In the rainy season all the plant species except *Mayodendron igneum* and *Acacia pennata* had significantly lower leaf water capacity than those of dry season (Figure S1).

Do different functional groups differ in their use of fog water?

Our results show that lianas use more fog water compared with that of tree species (Table I, Figure 5), highlighting the importance of fog water to lianas in seasonal tropical forest. Chen *et al.* (2015) found that lianas used more deep soil water than trees in dry seasons in the same forest as the present study; however, they did not include fog as a water source of plants. The results of the present study are contrary to our hypothesis that the lianas might take up more soil water with their deeper roots. Nearly all the leaves of the lianas are distributed on the canopy; thus, there is greater potential for the leaves of liana to intercept and thus absorb fog water (Limm *et al.*, 2009; Eller *et al.*, 2013; Goldsmith *et al.*, 2013). The lianas also had higher leaf area on a given stem area than the trees (Gerwing and Farias, 2000; Zhu and Cao, 2009), which could confer to lianas greater proportion of fog water in their stems. Our results highlight the importance of fog water for the dry season water use of the liana species.

The deciduous species used more fog water in the dry season compared with those of the evergreen species (Table I), which was contrary to our hypothesis set at the start of the study that the evergreen trees might uptake more fog water than the deciduous trees. The two deciduous species *L. tomentosa* and *Mayodendron igneum* are in the first layer in the forest, while the two evergreen species *C. sumutranus* and *L. comberi* are in the second layer. So the leaves of the deciduous species have greater potential to obtain moisture during fog events. Deciduous trees also tend to have relatively higher leaf area per sapwood area than that of evergreen trees (Sobrado, 1993; Fu *et al.*, 2012). The deciduous trees were leafless at the time we made sampling. However, the leafless period of the deciduous tree was very short (~1 month); the fog water might be previously uptaken by leaves of the deciduous species and then was stored in the xylem. There are direct evidences that the water absorbed by leaves can be transported to stem and below ground part (Eller *et al.*, 2013; Ishii *et al.*, 2014). At the beginning of the

dry season, the deciduous trees could uptake more fog water through leaves than evergreen trees, while the evergreen trees have leaves during the dry season and continuously uptake fog water and thus could totally use more fog water during the whole dry season. Thus, totally evergreen trees could use more fog water, but deciduous trees would absorbed more fog water at the beginning of dry season.

The percentage of fog water used by seedlings is among the range of study of Liu *et al.* (2014) but is lower than that of redwood forest of northern California (Dawson, 1998). The fog in northern California is much heavier than that of the present study (Dawson, 1998; Liu *et al.*, 2004). The seedling fog water use is also lower than that of Liu *et al.* (2010) from a non-karst forest nearby. However, the seedlings in Liu *et al.* (2010) are were less than 2 years and <15 cm height and the rooting depths were less than 8 cm. Thus, the seedling would mainly depend on the shallow soil water. However, the height of the seedling in our study was about 60–70 cm, and with rooting depth greater than 50 cm. Seedlings in the present study used the lowest proportion of fog water compared with other plant groups (Table I). The seedlings are the understory and thus have the smallest potential to intercept fog water. However, the understory seedlings are more likely to take up fog water from the shallow soil contributed by fog drip from the canopy leaves (Liu *et al.*, 2005).

CONCLUSIONS

All studied plant species in the Xishuangbanna tropical karst forest used fog water for transpiration during the dry season. Lianas used more fog water than tree species. Deciduous trees could use more fog water than the evergreen trees at the beginning of dry season when they maintain the leaves. Leaves of all six studied plant species have a potential to absorb fog water. The present study highlight the importance of dry season fog water for the plant species in an Asian tropical karst forest, showed that different functional groups have different capacity in using dry season fog water.

ACKNOWLEDGEMENTS

We acknowledge Ma Hong for field assistance and Dr Guang-Hui Lin for useful advice in sampling and analyzing the stable isotope data. We acknowledge Dr Ya-Jun Chen for useful comments to this manuscript. We acknowledge the two anonymous reviewers for their important and useful comments to our manuscript. The Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies provided the climate data. This work was supported by a major '973' project from the Chinese Ministry of Science and Technology (2006CB403207) and the National Natural Science Foundation of China (31300333), as well as '135' Program from Chinese Academy of Sciences (XTBG-F01).

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