

Plasticity of source-water acquisition in epiphytic, transitional and terrestrial growth phases of *Ficus tinctoria*

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ABSTRACT

Despite continued studies on the ecology and physiology of strangling hemiepiphytes, there is little quantitative information about the variations in source-water uptake by these species under different growth phases. In this study, the water acquisition patterns of a hemiepiphyte, *Ficus tinctoria*, is investigated in relation to growth phase (epiphytic, transitional and terrestrial) and season (foggy, hot-dry and rainy). Stable isotope compositions of water in xylem, soil, canopy humus, fog and rainfall were sampled on seasonally distinct dates, and soil water content and leaf carbon isotope composition were measured in order to determine the proportion of different water sources. Results indicated that *F. tinctoria* displayed a high degree of plasticity in source-water acquisition associated with the growth-phase transition from purely canopy-rooted epiphyte to transitional plant to terrestrial tree. During the foggy season and the hot-dry season, epiphytes utilized a combination of recently received rainwater (82–89%) and fog water (11–18%) present in canopy humus soil, whereas terrestrial trees exclusively depended on shallow and deep terrestrial soil water and exhibited marked flexibility in depth of soil water uptake. Transitional-phase plants relied predominantly on shallow soil water (79–86%) and extracted only a small fraction of canopy humus water (14–21%). During the rainy season, epiphytes relied almost exclusively on recent rainwater (96%) and had a negligible water uptake from fog, whereas trees extracted their water primarily from the shallow soil and less from the deep soil. Plants in transitional-phase drew a considerable fraction of water from canopy humus soil. This plasticity of source-water uptake to cope with radical changes in rooting environment is likely the key feature enabling hemiepiphytic species to thrive and successfully establish in the tropical rainforests. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS canopy humus soil; growth phases; soil water; strangler fig

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INTRODUCTION

Ficus species are one of the most important components of both lowland and montane forests throughout the tropics, and their interactions with many plant and animal species make them an ecologically important group (Daniels and Lawton, 1991; Williams-Linera and Lawton, 1995). There are about 800 *Ficus* species, including shrubs, climbers and trees, of which, about 500 species have hemiepiphytic habits (Berg, 1989). The hemiepiphytic growth form includes plants that germinate and grow as epiphytes but subsequently establish substantial and permanent rooting connections in the terrestrial soil (Putz and Holbrook, 1989). The most conspicuous of these in terms of habitat breadth, number of species and biomass are the strangler figs (Harrison *et al.*, 2003). These plants take their name from the anastomosing growth of their roots, which enclose

the host tree in a solid sheath, enabling the strangler to become a free-standing tree (Holbrook and Putz, 1996b).

Hemiepiphytes play a very important role in canopy dynamics by competing with their host tree species for water, light and nutrients, and stabilizing mats of epiphytic organic soil (i.e. canopy humus) that affect rainfall interception and ecosystem hydrology (Williams-Linera and Lawton, 1995; Benzing, 1998; Bruijnzeel, 2001). Hemiepiphytes commonly undergo a tri-phasic development in growth stage, from an epiphyte through to a terrestrial tree. Epiphyte is defined as plants lacking any root in contact with the ground and terrestrial tree as large, free-standing individuals that are reproductively mature (Holbrook and Putz, 1996b). Transitional-phase plants are distinguished from epiphytes by connecting roots in both the floor and canopy humus soil (Feild and Dawson, 1998). Although not parasitic, hemiepiphytes are dependent on host trees for establishment and support, with some species eventually forming extensive coalescing root systems that are capable of self-support (Todzia, 1986). The water sources used for growth and development potentially change as these hemiepiphytes make the transition from a purely epiphytic lifestyle to an

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arborescent one when the root connection to the ground is first established and access to terrestrial water and nutrient supplies first occurs (Laman, 1995; Zotz *et al.*, 1997). The epiphytic environment is characterized by unpredictable and severe episodes of low substrate moisture availability, and epiphytes must exhibit physiological and morphological traits that enable them to withstand intermittent drought (Holbrook and Putz, 1996b; Benzing, 1998). Studies of water relations and carbon economy in *Ficus* species showed that the evolution of epiphytic growth habit involved profound changes in a suite of intercorrelated ecophysiological traits even during the later terrestrial growth phase (Hao *et al.*, 2011a, 2011b). While atmospheric conditions experienced by individual plants often remain the same, hemiepiphyte access to water is greatly increased when epiphytic-phase plants become rooted in the ground (Holbrook and Putz, 1996a; Zotz *et al.*, 1997). Hence, the strangling hemiepiphytes provide an excellent 'natural experiment' on the effects of water availability on phenology, growth and habitat preferences (Putz and Holbrook, 1989), and comparative studies of the epiphyte-to-tree transition may provide important information to better understand the great success of hemiepiphytes in tropical rainforests (Feild and Dawson, 1998).

Despite continued studies on the ecology and physiology of strangling hemiepiphytes (Sternberg *et al.*, 1987; Ting *et al.*, 1987; Laman, 1995; Harrison *et al.*, 2003; Hao *et al.*, 2011a, 2011b), there is little quantitative information about the variations in source-water acquisition by these species under different growth phases (but see Holbrook and Putz, 1996a; Zotz *et al.*, 1997; Feild and Dawson, 1998; Wang *et al.*, 2010). In this study, the water acquisition patterns of a strangler fig, *Ficus tinctoria*, growing in a common garden is investigated in relation to growth phase (epiphytic, transitional and terrestrial) and season (foggy, hot-dry and rainy). The objective of this study is to determine any seasonal differences in water source among the three growth phases of *F. tinctoria*. We asked the following questions: (i) during the dry season (i.e. the foggy season and the hot-dry season), do canopy-rooted epiphytes acquire water from fog and from recent rainfall present in canopy humus soil? (ii) do transitional-phase plants acquire water from both canopy humus soil and terrestrial soil because they have roots both in the canopy and on the ground? and (iii) are differences in xylem isotopic 'signatures' between the three growth phases insignificant during the rainy season when water in canopy humus soil and terrestrial soil is plentiful and is recharged very frequently by current rain events?

MATERIALS AND METHODS

Study site and plant materials

The study was conducted in Xishuangbanna Tropical Botanical Gardens (XTBG; 21°55'39"N, 101°15'55"E,

560 m a.s.l.) of the Chinese Academy of Sciences, which is located in Menglun, Yunnan Province, Southwest China. This region has a seasonally dry tropical climate with two air masses alternating during the year (Vogel *et al.*, 1995). During the May–October rainy season, the southwest monsoon delivers about 80–90% of the annual rainfall, whereas the dry and cold air of the subtropical jet streams dominates the climate during the November–April dry season. The dry season also includes a foggy subseason from November to February, which is characterized by the highest frequency of dense radiation fogs during the night and morning, and a hot-dry subseason from March to April, which is characterized by dry and hot weather during the afternoon and with dense radiation fogs in the early morning. Radiation fogs occur nearly every day during the foggy season (Figure 1) and are heaviest from midnight (23:00–02:00) until midmorning (10:00–11:00). It was estimated that the contribution from fog water to the annual water input is about 5% in the local rainforest. Climate records for the past 40 years show that the mean annual air temperature is 21.7 °C, with monthly means ranging from 15.9 °C in January to 25.7 °C in June. The mean annual rainfall is 1480 mm, of which 87% occurs in the rainy season versus 13% in the dry season (Liu *et al.*, 2005).

The soil is about 2 m deep, well drained with a clay loam texture (42% coarse sands, 34% silts and 24% clays). The soil is classified as a Ferralic Cambisol (FAO/UNESCO) developed from alluvial deposits derived from sandstone, with an ochric A horizon and a cambic B horizon with ferralic properties (Vogel *et al.*, 1995). The parent material at a depth of 2 m consists of a 30–40 cm thick layer of gravel deposited by a side branch of the Upper Mekong River.

Ficus tinctoria Frost. f. subsp. *gibbosa* (Bl.) Corner is a hemiepiphyte that is commonly found in the rainforests of Xishuangbanna (Zhu *et al.*, 2006; Hao *et al.*, 2010). Some individuals of *F. tinctoria* eventually form extensive coalescing root systems that are capable of self-support,

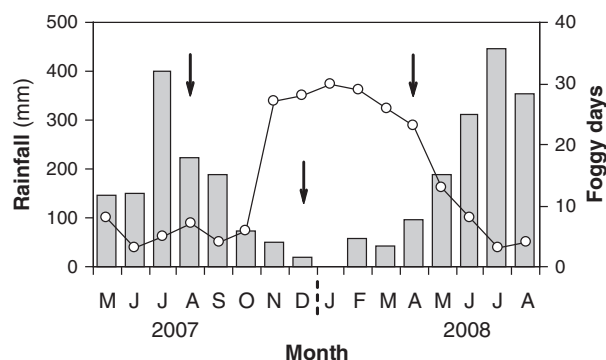


Figure 1. Monthly rainfall amount (bars) and foggy days (line) over the rainy/dry season of 2007–2008 at a weather station near the experimental site. Vertical arrows indicate sampling dates (i.e. on 11 August 2007, 21 December 2007, and 20 April 2008).

although some fall down if the host tree dies and rots away (Todzia, 1986; Hao *et al.*, 2011a). All plants sampled are from relatively open habitats and homogeneous soil, providing a similar environment and a common host species for the comparative analysis of variation in source-water use among the three growth phases. The most common host species of *F. tinctoria* at XTBG is the palm *Elaeis guineensis* Jacq.; nearly half of the palms support either an epiphytic or a ground-rooted *F. tinctoria* plant. Palms are particularly suitable host species for the study of strangler figs because their relatively small crowns cast little shade and because roots of epiphytic individuals cannot access the soil through an internal cavity in the host stem such as often occurs with dicotyledonous hosts (Holbrook and Putz, 1996a). The use of common garden plants also minimized plastic adjustments to local site conditions and guaranteed that the potential variations in plant source-water use can be attributable to growth phase rather than environmental differences (Hao *et al.*, 2011b).

Water, plant and soil sampling

To determine the sources of water used by *F. tinctoria*, all available water sources (fog water, rainfall, canopy humus water and terrestrial soil water at several depths) were sampled and their isotopic compositions (δD and $\delta^{18}\text{O}$) determined. Samples for main rain events were collected at a weather station (about 700 m southwest from the study site) from August 2007 to May 2008. Rainfall samples were collected immediately from a rain gauge after rain ceased or in the early morning when rain fell overnight. Four V-shape troughs (each 0.3×2.0 m), each connected to a plastic bottle, were mounted 0.7 m above the ground beneath the sampled host trees to collect fog water dripping from the canopy. The depth of the trough is 0.3 m. The troughs were read daily and were cleaned of any litter present. Fog water sampling was performed weekly. To ensure isotopic fractionation had not occurred, fog water sampling was performed at or near the peak of a fog drip event (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.*, 2005). Hence, water collected by the troughs comes from fog drops only. Samples of rainfall and fog water were stored in 10-ml screw-cap glass vials, wrapped in parafilm and frozen for later analysis.

Samples of plant xylem, terrestrial soil and canopy humus soil were collected on seasonally distinct dates, i.e. 11 August 2007 in the rainy season, 21 December 2007 in the foggy season and 20 April 2008 in the hot-dry season (Figure 1). At midday on each sampling date, plant xylem samples were taken from each of four epiphytes (each growing on a different palm), three transitional plants (each growing on a different palm) and three terrestrial trees of *F. tinctoria* within a 400 m long and 300 m wide

section at XTBG. The same plants were sampled on the three sampling dates. For each sample, xylem tissues were obtained by cutting three suberized mature stem segments. All green tissue was removed from these stems to avoid contamination of xylem water by isotopically enriched water (Dawson, 1998; Ehleringer *et al.*, 2000). This methodology, assuming that evaporative processes have not affected plant water in non-photosynthetic tissue, permits the analysis of water taken up by roots (Corbin *et al.*, 2005). Upon collection, the clipped stem samples were immediately placed in 10-ml glass vials, tightly closed with Teflon-sealed caps, wrapped in parafilm and kept in a cooler with ice in the field and kept frozen (-20°C) in the laboratory. Terrestrial soil samples were collected with a 4-cm diameter hand-operated auger. On each sampling date, three locations beneath the selected host tree crown were randomly chosen, and soil samples were collected from depths of 5, 20, 35, 50, 80, 100 and 120 cm at each location. Soil collections were centred at each sampling depth. Canopy humus soil samples were obtained by removal of debris by hand that had collected behind the tangle of *F. tinctoria* roots in the leaf axils of each host tree (i.e. behind the marcescent leaf bases of *E. guineensis*). Samples of canopy humus soil and terrestrial soil were collected at midday and weighed immediately, and water content [(soil water content) SWC, %] was determined by subtracting the dry mass after drying at 105°C for 48 h. Concurrently, the isotopic compositions of water in the canopy humus soil and in the terrestrial soil profile were sampled by taking humus soil and sequential soil cores. These samples were stored as previously described for stem samples.

Fully expanded, sun-exposed leaves on each sampled epiphyte, transitional plant and terrestrial tree were collected during each of the three sampling seasons to determine carbon isotope ratio ($\delta^{13}\text{C}$). Individuals producing new leaves can be found throughout the year, although peaks in leaf expansion coincide with the rainy season (Putz and Holbrook, 1989; Hao *et al.*, 2010). We selected leaves that appeared to have expanded during each sampling season. The leaves were dried at 70°C for 24 h and finely ground for later isotope analysis.

Water was extracted from plant xylem, canopy humus soil and terrestrial soil samples using a cryogenic vacuum distillation method (Ehleringer *et al.*, 2000). The δD and $\delta^{18}\text{O}$ of the fog water, xylem water, soil water, rainfall, and canopy humus water and leaf $\delta^{13}\text{C}$ were measured using an isotope ratio mass spectrometer (Thermo Finnigan, USA) at the Stable Isotope Facility, Chinese Academy of Forestry, with accuracies of $\pm 1.5\text{‰}$, $\pm 0.2\text{‰}$ and $\pm 0.5\text{‰}$ for δD , $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, respectively. Isotope ratios of hydrogen and oxygen were expressed in δ units relative to Vienna Standard Mean Ocean Water, whereas carbon isotope ratio was relative to Pee Dee Belemnite standard (Ehleringer *et al.*, 2000).

Data analysis

Isotope values of potential water sources and xylem water were analysed with the IsoSource mixing model (Phillips and Gregg, 2003) to evaluate the relative contribution of each source to xylem water content. To avoid misrepresenting the results, results are reported as the distribution (i.e. minimum to maximum) of feasible solutions rather than focusing on a mean value. For terrestrial trees, soil profiles were subdivided into three depth intervals (<20, 20–50 and >50 cm) to facilitate comparison of the potential water sources. Although these depths differ in range, they were selected on the basis of SWC inspection and analysis of soil water isotope profile. The isotopic composition for each soil depth interval was determined using the water content-weighted mean approach (Snyder and Williams, 2003; Ogle *et al.*, 2004; McCole and Stern, 2007). Generally, the shallow soil water is derived from recent rainfall, whereas the old water in the deep soil layers came from the previous rainfall (mostly during the rainy season) (Barnes and Turner, 1998). For transitional-phase plants, the two upper soil depth intervals (i.e. <20 and 20–50 cm) and the canopy humus soil (containing recent rainfall and fog water) were considered as the potential sources because root connection to the ground is exclusively restricted to the upper-level terrestrial soil (<50 cm) and access to terrestrial water supplies first occurs in their early establishment (Zotz *et al.*, 1997). In the rainy season, however, the isotope profile in soil does not show a gradient from surface to deeper layers (see Results section in the succeeding text), which makes it impossible to apply the IsoSource mixing model with isotope values (Burgess *et al.*, 2000) for the transitional-phase plants and terrestrial trees. In this case, comparisons of the isotopic compositions of stem water and potential sources of soil water at different depths were only made to identify the most probable sources of water uptake (Asbjornsen *et al.*, 2008).

Because epiphytic-phase plants have roots only in the canopy humus, we were interested in quantifying the fractional input of recently received rainfall and fog water (present in canopy humus soil) to the xylem tissue. These fractional inputs were determined using a simple two-end-member linear mixing model with $\delta^{18}\text{O}$ values to calculate the proportion of recent rainfall (P_r) in epiphytic plant stem tissue (adapted from Dawson, 1993):

$$P_r = (\delta X_e - \delta X_f) / (\delta X_r - \delta X_f) \quad (1)$$

where δX_e is the isotopic value of epiphyte xylem water, δX_f is the isotopic value of fog water and δX_r is the isotopic value of rainfall. In this analysis, the $\delta^{18}\text{O}$ value of last rainfall before each sampling date was defined as δX_r , and the average $\delta^{18}\text{O}$ value of fog water sampled during the sampling month was defined as δX_f .

Statistical analyses were conducted using the programme SPSS 13.0 (SPSS Inc., Chicago, USA). A factorial analysis of

variance (ANOVA) contrasting growth phase (epiphytic, transitional and terrestrial) and season (foggy, hot-dry and rainy) was carried out to detect the significance of main effects (growth phase and season) and interactions between growth phase and season on xylem water isotope and leaf $\delta^{13}\text{C}$ after testing for normality of residuals and homogeneity of variances. Seasonal patterns of soil water isotope and SWC were investigated with an ANOVA with season and soil depth as factors. Significant differences among xylem water isotope and leaf $\delta^{13}\text{C}$ between growth phases were detected using one-way ANOVA followed by *post hoc* Fisher's least significant difference test.

RESULTS

Soil moisture and isotopic composition

Soil water content underwent pronounced seasonal changes down to 120 cm depth, with the lowest values in the hot-dry season and highest values in the rainy season (Figure 2). Soil moisture increased with depth in the hot-dry and foggy seasons but not in the rainy season when there was a higher SWC near the soil surface compared with the deep layer. There was a significant effect of season ($P < 0.001$), depth ($P = 0.031$) and season \times depth interaction ($P = 0.036$) on SWC. However, no significant difference was found in SWC between the foggy season and the hot-dry season ($P = 0.216$).

During the foggy season and the hot-dry season (Figure 2), water contents of canopy humus soil were highly variable and substantially higher than those of each corresponding shallow soil (0–50 cm; $P < 0.05$) but similar to each other ($P = 0.118$). During the rainy season, moisture

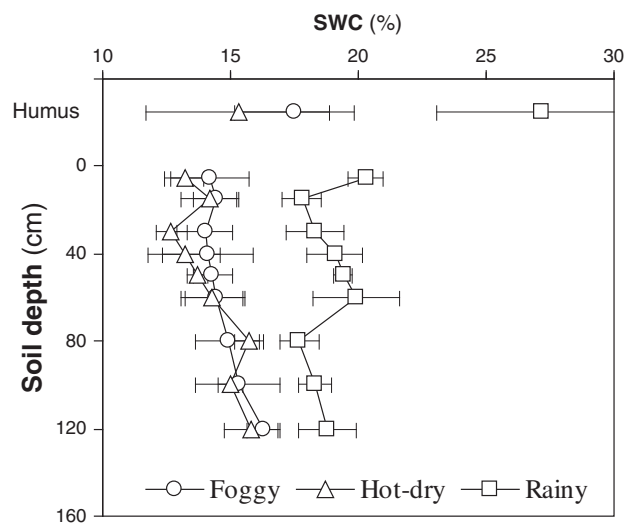


Figure 2. Water contents of canopy humus soil and terrestrial soil (SWC) profile at the experimental site on seasonally distinct dates, i.e. 11 August 2007 in the rainy season, 21 December 2007 in the foggy season, and 20 April 2008 in the hot-dry season. Horizontal crossed bar represents ± 1 standard error ($n = 3$).

levels of canopy humus soil ranged from 17% to 43%, significantly higher than during the foggy season and the hot-dry season ($P < 0.001$) and significantly higher than those of the soil profile ($P = 0.002$). Moisture content values in canopy humus soil also showed large standard errors, reflecting the extreme heterogeneity of substrate moisture behind the palm leaf bases and the frequent limitations of water availability for epiphytes.

The isotope ratios of water in terrestrial soil, rainfall, fog, plant xylem and canopy humus soil are plotted in Figure 3 along with the local meteoric water line ($\delta D = 7.96\delta^{18}O + 8.67$; Liu *et al.*, 2005). As the soil and humus samples were subject to free evaporative processes, these were plotted along and slightly to the right of the local meteoric water line and conformed to the equation $\delta D = 6.19\delta^{18}O - 12.90$ ($R^2 = 0.688$, $P < 0.05$), suggesting that the soil and humus had undergone considerable evaporation. There was a significant effect of season, depth and season \times depth interaction on soil water isotope ($P < 0.001$). However, the difference in soil water isotope between the foggy season and the hot-dry season was not significant ($P = 0.857$). Isotopic ratios of soil water were enriched near the soil surface relative to deeper soil at every sampling period and reflected both the isotopic ratios of recent precipitation and evaporative fractionation (Figure 4). In the rainy season, the negative isotope values near the surface likely resulted from the combined effects of recent inputs of isotopically depleted monsoon rainfall, isotopic enrichment of soil water by evaporation and mixing of rainwater and soil water previously enriched by evaporation. In contrast, the other two sampling dates were preceded by relatively dry conditions, which would have favoured the establishment of a stable isotope gradient in the soil profile through strong evaporative

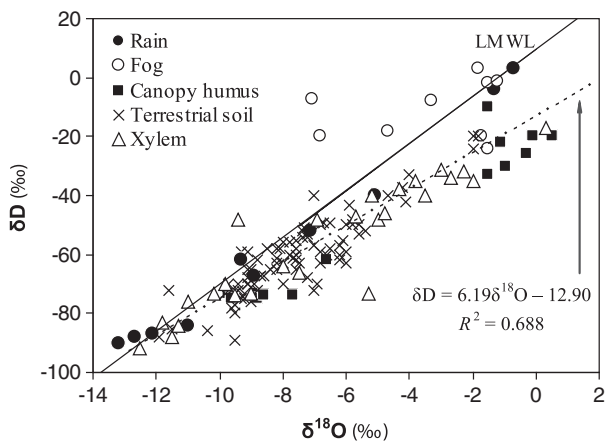


Figure 3. Plot of δD versus $\delta^{18}O$ of water in rainfall, fog, terrestrial soil and canopy humus soil in comparison with plant xylem water of *Ficus tinctoria* collected at the experimental site shown with the local meteoric water line (LMWL). Regression line (dotted) drawn through the terrestrial soil and canopy humus soil data.

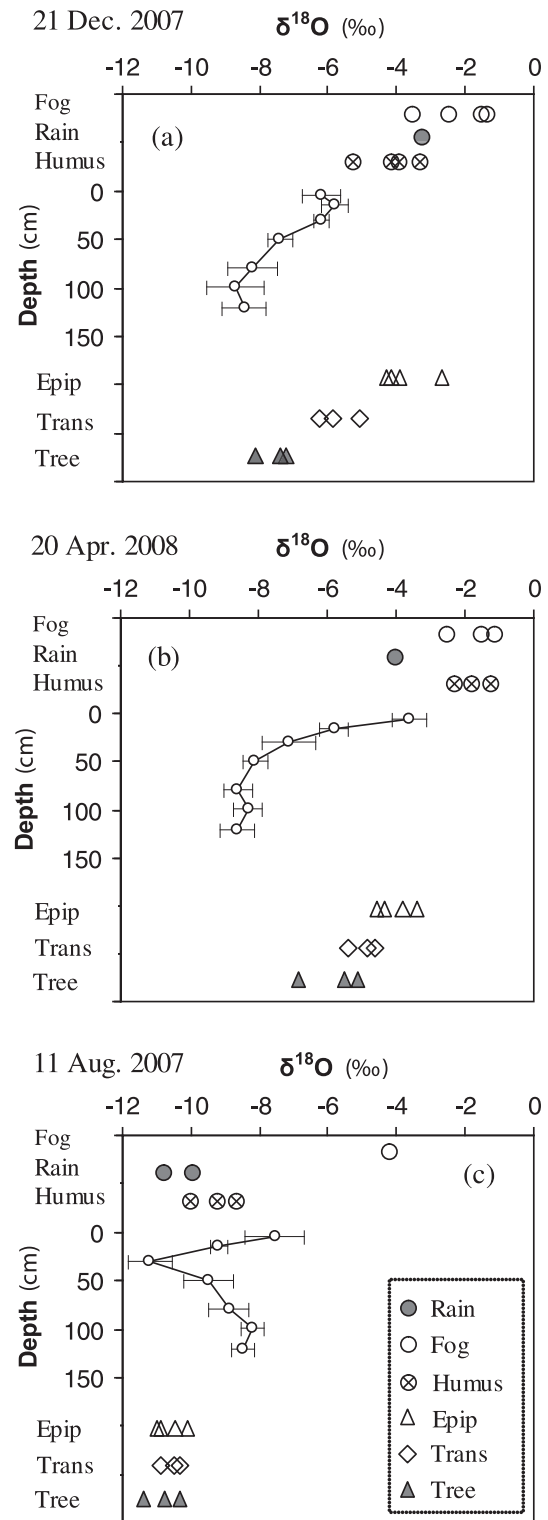


Figure 4. Vertical profiles of soil water $\delta^{18}O$ at the experimental site on (a) 21 December 2007 in the foggy season, (b) 20 April 2008 in the hot-dry season and (c) 11 August 2007 in the rainy season. $\delta^{18}O$ values of plant xylem water collected from epiphytic (Epip), transitional (Trans) and terrestrial (Tree) individuals of *Ficus tinctoria* are shown at the bottom of each panel, whereas values for fog water, recent rainfall (collected before the plant sampling date) and canopy humus water are shown at the top of each panel. Horizontal crossed bar represents ± 1 standard error ($n = 3$).

enrichment, although the other processes are still present (Barnes and Turner, 1998; Brooks *et al.*, 2010).

During the foggy season, significant differences in isotope ratios were observed between canopy humus water and fog water ($P=0.048$), with the latter being more enriched [Figure 4(a)]. During the hot-dry season, canopy humus water had isotope values more enriched than that of recent rainfall ($P=0.011$) but similar to fog water [$P=0.811$; Figure 4(b)]. No difference in isotope values was found between canopy humus water and recent rainfall during the rainy season [$P=0.749$; Figure 4(c)].

Seasonal differences in source-water acquisition

The isotope values of *F. tinctoria* xylem water were plotted around the regression line of terrestrial soil water and canopy humus water (Figure 3) and conformed to the equation $\delta D = 5.52\delta^{18}O - 19.29$ ($R^2 = 0.875$, $P < 0.05$), suggesting that xylem water was mainly acquired from those two water sources. Xylem water isotope ratios were significantly affected by season, growth phase and season \times growth phase interaction ($P < 0.001$). There was a consistent trend in xylem isotope values during the foggy season and the hot-dry season ($P < 0.05$), with the highest values in epiphytes and lowest values in terrestrial trees [Figure 4(a) and (b)]. However, consistent with our initial assumption, the three growth phases did not differ significantly from one another in xylem isotope values in the rainy season [$P > 0.05$; Figure 4(c)].

During the foggy season, xylem isotope values of epiphytic-phase plants were plotted within the range of fog water and recent rainfall [Figure 4(a)], suggesting that epiphytes were reliant on these two water sources. According to the two-end-member model calculations (Table I), epiphytes acquired substantially large proportions of recent rainfall (82%) and relied little on available moisture from fog (18%). In contrast, the tree isotope

values, which differed significantly from epiphyte and transitional plant values, corresponded only to that of deep soil water (>50 cm), indicating that greater water uptake from this soil layer had occurred. The IsoSource model predicted that terrestrial trees with the smallest xylem $\delta^{18}O$ values derived 53% of their water from soils deeper than 50 cm, although the shallow soil layer (<50 cm) was also a significant source of moisture. Consistent with our expectations, the transitional plant isotope values were somewhere between the shallow soil water and canopy humus water signatures, suggesting that they extracted a mixture of canopy humus and shallow soil water sources. Results from the mixing model analyses showed that once a root connection was made to the terrestrial soil, transitional plants predominantly depended on shallow soil water (30% from <20 cm depth and 56% from 20–50 cm depth) and took up only a small proportion of their water from canopy humus soil (14%).

During the hot-dry season, isotope values of transitional plant and tree followed similar patterns as in the foggy season, being somewhere between the shallow soil water and canopy humus water signatures in transitional plants and closer to that of deep soil water in trees. However, the main depth of soil water uptake by these two growth phases appeared to have shifted to somewhat shallower levels in the soil profiles compared with the previous foggy season, which likely resulted from recent rainwater input to the shallow soil before the plant sampling date [Figure 4(b)]. Soil water isotope values within 0–20 cm depth were consistent with that of recent rainfall ($P > 0.05$), implying that soil water had been recharged by this rain event, as mirrored by an increase in SWC at 20 cm depth in the soil profile (Figure 2). Consequently, water uptake from the shallow soil layers by transitional plants and trees increased considerably in comparison with the previous foggy season (Table I). Similarly, the use of canopy humus water by

Table I. Proportions of feasible water sources (%) for epiphytic (Epip), transitional (Trans) and terrestrial (Tree) growth phases of *Ficus tinctoria* at the experimental site on seasonally distinct dates.

Water source ^a	21 December 2007 (foggy season)			20 April 2008 (hot-dry season)			11 August 2007 (rainy season)		
	Epip	Trans	Tree	Epip	Trans	Tree	Epip	Trans	Tree
Rain	82	—	—	89	—	—	96	—	—
Fog	18	—	—	11	—	—	4	—	—
Canopy humus	—	14 (0–28)	—	—	21 (0–46)	—	—	np	—
Soil <20 cm	—	30 (5–82)	19 (0–47)	—	38 (0–65)	33 (24–38)	—	np	np
Soil 20–50 cm	—	56 (19–79)	28 (3–86)	—	41 (34–54)	27 (0–60)	—	np	np
Soil >50 cm	—	—	53 (14–81)	—	—	40 (0–76)	—	—	np

^a For epiphytes, the average source proportions were estimated with a two-end-member mixing model (Dawson, 1993), whereas for transitional plants and terrestrial trees in the foggy season and hot-dry season, they were estimated with the IsoSource mixing model (Phillips and Gregg, 2003) and shown with the range of minimum/maximum proportions (in parentheses). In the rainy season, however, the isotope profile in soil does not show a gradient from surface to deeper layers [Figure 4(c)], which makes it impossible to apply the IsoSource model with isotope values (Burgess *et al.*, 2000). np represents impossible to calculate.

transitional plants increased remarkably owing to the channelling of recent rainwater into the canopy substrate by palm leaf bases. The epiphyte isotope values were within the range of recent rainfall and fog water signatures, and the model predicted that epiphytes had little water uptake from fog moisture (11%) and relied primarily on recent rainfall (89%).

During the rainy season, when rainfall was most frequent, soil water isotope values were irregular and overlapped in two soil depths, and plant values did not clearly indicate the water sources of the transitional plants and trees [Figure 4(c)]. Although we can not apply the IsoSource model to evaluate the relative contribution of each source, the isotope ratios of transitional plants and trees all appeared to match soil water values at the shallow layer (<50 cm), whereas those of epiphytes were very similar to that of recent rainfall. We inferred that water of transitional plants and trees might have been predominately acquired from the shallow soil layer. Indeed, also by applying the two-end-member mixing model with isotope values of canopy humus water and shallow soil water (<50 cm) for the transitional plants, it was estimated that the contribution from canopy humus water to the plant is only 31%. As such, the primary water source for the transitional plants was shallow soil water. Because few fog events occurred during the rainy season and rainfall was the mainly potential source of canopy humus water, the proportion of rainfall to epiphyte xylem water was estimated to be 96%, with fog water being negligible.

Leaf carbon isotope ratios

Leaf $\delta^{13}\text{C}$ in epiphytic-growth, transitional-growth, and tree-growth phases of *F. tinctoria* ranged from -28.1‰ to -32.7‰ , with the epiphytic phase being more variable in the hot-dry season (Figure 5). There was no significant effect of season, growth phase and season \times growth phase interaction on leaf $\delta^{13}\text{C}$ values ($P > 0.05$). During the hot-dry season, leaf $\delta^{13}\text{C}$ values between the three growth phases were not significantly different from one another ($P > 0.05$), although values in the canopy-rooted epiphytes were slightly higher than in the transitional plants and terrestrial trees. No significant difference in leaf $\delta^{13}\text{C}$ was found between the three growth phases during the foggy season and the rainy season ($P > 0.05$).

DISCUSSION

Hemiepiphytic *F. tinctoria* displayed a high degree of plasticity in source-water acquisition associated with the growth-phase transition from epiphyte to transitional plant to terrestrial tree. Consistent with our initial assumption, each growth phase acquired different water resources.

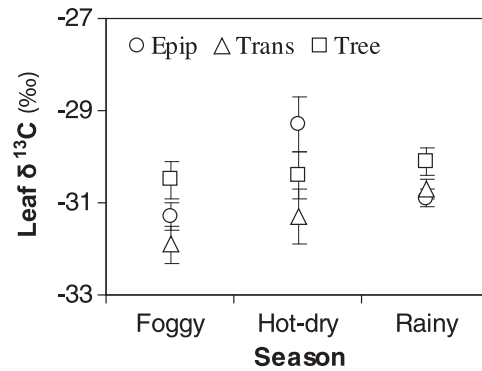


Figure 5. Carbon isotope ratios ($\delta^{13}\text{C}$) of recently expanded leaves collected from epiphytic (Epip), transitional (Trans) and terrestrial (Tree) individuals of *Ficus tinctoria* at the experimental site on seasonally distinct dates, i.e. 11 August 2007 in the rainy season, 21 December 2007 in the foggy season and 20 April 2008 in the hot-dry season. Vertical crossed bar represents ± 1 standard error ($n = 3$).

During the foggy season and the hot-dry season, epiphytic *F. tinctoria* utilized a combination of recently received rainwater and fog water trapped by canopy humus soil. Once a root connection was made with the ground, transitional individuals predominantly relied on water in shallow soil layers from recent rain events (79–86%) and extracted only a small fraction of their water from canopy humus soil (14–21%). These results are comparable with the observations in a tropical cloud forest of Costa Rica, where *Didymopanax pittieri*, a hemiepiphytic species that undergoes similar growth-phase changes, exhibited a similar pattern in source-water utilization (Feild and Dawson, 1998). However, compared with the fog water acquisition of epiphytic *D. pittieri* (76% of water obtained from fog/cloud), epiphytic *F. tinctoria* at our site had quite small fractions of water uptake from fog moisture (11–18% in the dry season). The apparent low uptake of fog water by epiphytic *F. tinctoria* could be attributed to low wind speed ($< 1.0 \text{ m s}^{-1}$) during fog event and the low liquid water content (LWC) of radiation fog at our study site (Liu *et al.*, 2005). Under low wind speeds and low LWC, which are typical for radiation fog, sedimentation is the dominant process of fog deposition (Lovett, 1984; Glasow and Bott, 1999), whereas at higher wind speeds ($> 5.0 \text{ m s}^{-1}$) and higher LWC, deposition via impaction (i.e. fog interception by leaves) greatly increases (Asbury *et al.*, 1994). This suggests that for epiphytic *F. tinctoria* at our site, the available fog water that is intercepted by host palm leaves and then funnelled into the epiphytic substrate by palm leaf bases is relatively low, which is supported by our observations on days with dense radiation fog when only a small proportion of the upper trunk of the host palm was occasionally saturated by the intercepted fog water. However, direct fog uptake through plant leaves may be important, although it is likely a smaller fraction than that taken up through roots (Hutley *et al.*, 1997; Burgess and

Dawson, 2004; Limm *et al.*, 2009; Ritter *et al.*, 2009). But this was not distinguished in our results and should be studied further.

The IsoSource model predicted a sizeable fraction of water uptake from both shallow and deep soil layers by *F. tinctoria* trees (Table I), suggesting that tree-phase plants exhibited a high degree of flexibility in depth of soil water uptake and may have had access to both deeper and shallower soil water sources throughout the year. This should result from a functionally dimorphic root system that preferentially acquires relatively consistent water from deeper soil but can alternatively consume shallower soil water, as shown elsewhere for other tree species (Lin *et al.*, 1996; Dawson, 1998; Williams and Ehleringer, 2000; Oliveira *et al.*, 2005; Querejeta *et al.*, 2007; Scholz *et al.*, 2008; Eggemeyer *et al.*, 2009; Verweij *et al.*, 2011; Yang *et al.*, 2011; Rossatto *et al.*, 2013). In contrast to the acquisition of more water from deeper soil layers by terrestrial trees during the foggy season, transitional plants in this season relied largely on shallow soil water (<20 cm; Table I). However, during the hot-dry season, water uptake from the upper soil layers (<20 cm) by both terrestrial trees and transitional plants increased remarkably, as demonstrated by their soil water and xylem water isotope values [Figure 4(b)], which likely resulted from a 31.8 mm pulse of rainfall 5 days prior to the sampling date (Figure 1). Several other studies conducted in seasonally dry tropical regions have also concluded that trees depend mostly on water stored within the upper soil profile during the dry season (Feild and Dawson, 1998; Drake and Franks, 2003; Nippert and Knapp, 2007; Goldstein *et al.*, 2008). Meinzer *et al.* (1999) also pointed out that the extensive horizontal area explored by a lateral root system may partially compensate for the reduced water content in the subsoil profile. During the rainy season, with the increase in water availability in the shallow soil profile, *F. tinctoria* trees extracted their water predominately from the shallow soil layers (<50 cm) and less from the deep soil layers. The greater lateral spread of tree roots in the upper soil layer may compensate for limited access to water stored within the deeper soil layer, as observed by Williams and Ehleringer (2000) in pinyon-juniper forests and Donovan and Ehleringer (1994) in a shrub community, who suggest that trees rely on shallower root water uptake where precipitation is relatively predictable. This shift from deep soil layers to shallow soil layers as major water sources appears to be very important for species growing in water-limited environments, especially in seasonally dry tropical regions (Querejeta *et al.*, 2007; Eggemeyer *et al.*, 2009).

It is interesting to note that while transitional *F. tinctoria* relied primarily on the more abundant and stable soil water reserves, they did not completely abandon the acquisition of canopy humus water derived from recent rainfall and fog water (Table I). Once epiphytic-phase plants become

rooted in the ground, transitional plant access to water is greatly increased, and by rooting in both canopy soil and terrestrial soil, these plants can more easily meet their great water demands (Holbrook and Putz, 1996a). Our data showed that although less canopy humus water was obtained by transitional plants during the dry season, a considerable fraction of this water might have been utilized during the rainy season because water stored in the canopy humus soil is particularly plentiful (Figure 2). Consistent with this finding, observations from Feild and Dawson (1998) showed that transitional *D. pittieri* acquired about one-third of the water from canopy soil.

Because strangling hemiepiphytes must grow as epiphytes, they may be restricted to particularly moist microsites within the canopy. Our measurements showed that the water content of canopy humus soil was highly variable during each sampling season (Figure 2), with some relatively moist microsites. This extreme heterogeneity of the substrates in the epiphytic rooting environment was also noted by Holbrook and Putz (1996a) and suggests both the availability of some moisture during the dry season and the possibility of intermittent depletion during the rainy season. Palm leaves may effectively funnel water towards the trunk, and even quite small/light rain events would be sufficient to saturate epiphyte rhizospheres (Putz and Holbrook, 1989). However, the water stored in the small volume of canopy humus soil is relatively limited, which would greatly diminish the amount of water acquisition by epiphytic individuals. In addition, the canopy humus soil is commonly exposed to the atmosphere and dries more rapidly than the terrestrial soil. This substantial drying may take place even between rains during the rainy season as well as during the dry season (Holbrook and Putz, 1996b). Therefore, the frequent and even severe episodes of low water availability would inevitably occur in the canopy environment, and epiphytes must exhibit physiological and morphological traits that enable them to withstand intermittent drought (Holbrook and Putz, 1996a). Indeed, recent observations from comparative physiology studies of hemiepiphytic and non-hemiepiphytic *Ficus* species at this study site revealed that the existence of an epiphytic habit during the juvenile stage in hemiepiphytic species involved a suite of leaf water flux and drought tolerance traits of functional importance, contrasting with those of congeneric non-hemiepiphytic species (Hao *et al.*, 2010, 2011a). Epiphytic strangler figs also appear to rely on a combination of strong stomatal control, maintenance of high leaf water potentials and perhaps some degree of stem water storage to cope with the fluctuating water regime of the epiphytic environment (Holbrook and Putz, 1996a).

Because plant leaf $\delta^{13}\text{C}$ largely reflects the ratio of assimilation to stomatal conductance, it has been widely interpreted as an integrated measure of water-use efficiency provided that leaves experience similar evaporative

conditions (Farquhar and Richards, 1984). The frequent water deficit in the epiphytic rooting environment indicates that epiphytes should be more efficient and more conservative in terms of their water use than conspecific trees rooted in the ground (Holbrook and Putz, 1996b; Hao *et al.*, 2011a). In our study, however, there were no significant differences in leaf $\delta^{13}\text{C}$ between the three growth phases of *F. tinctoria* in each season (Figure 5). Similarly, Holbrook and Putz (1996a) also found no differences in leaf $\delta^{13}\text{C}$ between growth phases of two hemiepiphytic species, *Ficus trigonata* and *Ficus pertusa*, in a Venezuelan palm savanna. Whereas an earlier study on strangler figs reported a higher dry season $\delta^{13}\text{C}$ value (more water-use-efficient) in epiphytic individuals compared with conspecific trees, with similar $\delta^{13}\text{C}$ values during the wet season (Ting *et al.*, 1987). It is possible that the degree of fractionation associated with respiration and translocation may differ between the growth phases, complicating interpretation of the $\delta^{13}\text{C}$ data (Farquhar *et al.*, 1989). Also, interpretation of the $\delta^{13}\text{C}$ data may be complicated by substantial differences in internal leaf structure and stomatal density between the growth phases, which could influence $\delta^{13}\text{C}$ values through an effect on mesophyll resistance (Holbrook and Putz, 1996b). Hence, a more intense sampling scheme is necessary to answer to this question because our data and those from others are quite limited or just based on a few times of observations (i.e. only 1 day in each season).

CONCLUSIONS

Ficus tinctoria displayed a high degree of plasticity in source-water acquisition associated with the growth-phase transition from purely canopy-rooted epiphyte to transitional plant to terrestrial tree. Epiphytes utilized a combination of recently received rainwater and fog water present in canopy humus, whereas terrestrial trees exclusively depended on shallow and deep terrestrial soil water and exhibited marked flexibility in depth of soil water uptake. Transitional plants relied predominately on water from shallow soil and extracted only a small fraction of water from canopy humus soil. This plasticity of source-water uptake to cope with radical changes in rooting environment is likely the key feature enabling hemiepiphytic species to thrive and successfully establish in the tropical rainforests.

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