

Vertical patterns of soil water acquisition by non-native rubber trees (*Hevea brasiliensis*) in Xishuangbanna, southwest China

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ABSTRACT

The rubber tree (*Hevea brasiliensis*) has been extensively cultivated in Xishuangbanna, southwest (SW) China. It shows strong synchronicity for flushing and shedding, displaying a very different phenology to the native vegetation. However, little is known about the water-use patterns of the plant in this area. We assessed seasonal water-use strategies of rubber trees over the course of a rainy/dry season cycle. Stable isotope compositions of water in xylem, soil, rain and groundwater were sampled on seasonally distinct dates, and soil water content, root distribution and leaf water potential on sunny days were measured in order to determine the proportion of water derived from different soil layers. Midday leaf water potential of rubber trees was relatively stable throughout the year and did not drop significantly during the late dry season, displaying isohydric behaviour. Soil and stem water isotope signatures along with rooting distributional patterns revealed that rubber trees extracted their water mostly from the top 30 cm and less from below 70 cm of the soil profile during the late rainy season when soil water was plentiful. During the late dry season, as the moisture in the middle soil layers (30–70 cm) was gradually depleted, the depth of water uptake shifted to deeper soil levels. Model calculations showed that the proportion of water uptake from the shallow soil layer (<30 cm) increased markedly after the most recent rainfall in the late dry season and the early rainy season (varying between 65% and 71%), indicating significant plasticity in sources of water uptake in this dimorphic-rooted species. This ability to take up a large proportion of shallow soil water after rainfall is likely the key feature enabling rubber trees to thrive through the period of greatest water demand. Our results suggest that rubber trees are able to adjust the allocation of resources and thus acclimate to the spatiotemporal changes to water conditions in the soil profile. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS pronounced dry season; rubber trees; stable isotope; water-use patterns

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INTRODUCTION

Many tropical forests experience a prolonged dry season with little or no rain, causing severe drying in shallow soil layers (Wei *et al.*, 2005; Goldstein *et al.*, 2008). Therefore, the distribution and accessibility of soil water greatly influences plant growth and survival (Drake and Franks, 2003). However, a variety of traits allow plants to persist under prolonged dry conditions, such as early flowering, leaf and stem succulence, and deep roots that access permanent water sources (Corbin *et al.*, 2005; Goldstein *et al.*, 2008). Many studies have found that dimorphic-rooted species derive most of their transpiration water from shallow soil layers in the wet season and more water from deep soil layers in the dry season (Lin *et al.*, 1996; Smith *et al.*, 1997; Burgess *et al.*, 2000;

Williams and Ehleringer, 2000; Andrade *et al.*, 2005; Nie *et al.*, 2012). The shift from shallow to deep layers as the major water source appears to be very important for species growing in water-limited environments (Dawson and Pate, 1996; Moreira *et al.*, 2000; Sternberg *et al.*, 2004).

Hevea brasiliensis (rubber tree), the single viable source of natural rubber, is a perennial crop that has economic and social importance in many tropical and subtropical areas in the world (George *et al.*, 2009). As a tree native to the tropical rainforest of the Amazon Basin, its ideal habitat is characterized by small variations in air temperature (24–28 °C) and precipitation (about 2000 mm) throughout the year and monthly rainfall of >100 mm (Vogel *et al.*, 1995). Rubber naturally occurs between 10° north and 10° south at a maximum altitude of 600 m a.s.l. (Guardiola-Claramonte *et al.*, 2010). However, in order to benefit from the increasing demand for natural rubber, the cultivation of *H. brasiliensis* has been extended to higher latitudes and altitudes in South America, Southeast Asia and Africa. Nowadays, the loss of

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primary and secondary natural forests is especially serious in the major rubber production areas of Southeast Asia, because they are located within the so-called Indo–Burma hotspot, one of the 34 global biodiversity hotspots. Consequently, in these marginally suitable environments (drier and colder), the productive life of rubber, its latex yield and its growth are greatly reduced (Vogel *et al.*, 1995; Chen and Cao, 2008; Isarangkool Na Ayutthaya *et al.*, 2011).

In Xishuangbanna, plantations of the cold-resistant rubber tree clone (PB86 and RRIM600, widely cultivated in this area) have replaced primary forest that grows up to 1100 m a.s.l. (Vogel *et al.*, 1995; Li *et al.*, 2008), well beyond the extremes of the native environment in the Amazon Basin. Nowadays, areas of this region have been replaced with more than 400 000 ha (i.e. >20% of the total land area) of rubber plantations to meet the insatiable market demand (Li *et al.*, 2008; Ziegler *et al.*, 2009). However, despite the large extension of land covered by rubber trees in the region, the environmental impacts of rubber expansion have only been explored recently at various scales (Chen and Cao, 2008; Guardiola-Claramonte *et al.*, 2008, 2010; Li *et al.*, 2008; Tan *et al.*, 2011). It is recognized that land-cover transitions to rubber tree monocultures may result in significant losses of aboveground (Bunker *et al.*, 2005) and belowground carbon stocks and biodiversity (Li *et al.*, 2008; Ziegler *et al.*, 2009). The conversion of native rainforests to rubber plantations is also believed to be the main cause of the dramatic downward trend in fog frequency and duration in recent years, because rainforests contribute the largest fraction of the sources in fog moisture, and rubber plantations can cause more surface run-off during the rainy season and less water shortage and evapotranspiration during the dry season (Liu *et al.*, 2007). Furthermore, although information on water-use characteristics is very limited, rubber trees have also been referred to as ‘water pumps’ as they are associated with water depletion in the basins where they are grown (Tan *et al.*, 2011). In fact, after several decades of rubber-tree planting, dry season surface water shortages, which seldom occurred previously even during the driest year, are frequently experienced by local people (Qiu, 2009). Clearly, a reliable assessment of the hydrological threat caused by rapid land-cover conversion to rubber tree requires new data, and studies of evapotranspiration and water-use patterns in rubber trees are becoming increasingly important (Ziegler *et al.*, 2009; Guardiola-Claramonte *et al.*, 2010).

In this study, the seasonal water-use patterns of non-native rubber trees was investigated by sampling the stable isotopic ratios ($\delta^{18}\text{O}$) of water in soil, rain, plant tissue (stem and superficial root) and groundwater, and by measuring soil water content (SWC), root distribution and leaf water potential over the course of a rainy/dry season cycle (2008–2009). The objectives of this study were to determine the proportional contribution of water from different soil depths to total water

uptake by rubber trees and to enhance our understanding of how changes in land use in this area have altered plant water uptake dynamics and the implications for hydrologic functioning in this landscape. We selected a mature representative rubber tree stand within a typical catchment containing the most widely planted clone (clone PB86) in Xishuangbanna. This catchment is located in the central part of this area where rubber trees have been regularly exposed to soil and atmospheric drought. We hypothesized that (i) rubber trees utilize water primarily from greater depths in the soil profile and greatly deplete the subsoil water; (ii) the water source will differ between seasons, i.e. switch from shallow (in the rainy season) to deep (in the dry season) soil water; and (iii) trees growing on upslope tap deeper soil water than those growing on the downslope, thus circumventing the problem of limited water supply from the shallow soil layer during the pronounced dry season.

MATERIALS AND METHODS

Site description

The study site is located in the Xishuangbanna Tropical Botanical Garden (XTBG; 21°55′39″N, 101°15′55″E) in Yunnan Province, SW China. Observations were conducted in a small catchment (19.3 ha) covered with a 20-year-old rubber monoculture plantation, which is a typical catchment in this area with a gently sloping geomorphology. The catchment spans an altitudinal range of 560–730 m a.s.l. with an average slope of 16° and yields a small perennial stream flowing from northwest to southeast. The rubber trees were planted at 2.1 m × 4.0 m spacing (370 trees ha⁻¹) on level bench terraces on the catchment slopes after complete clear-cutting of primary forest in 1987/1988 and received uniform agro management (i.e. control of understory growth, fertilization, latex extraction etc.) and tapped for latex for 11 years. Mean diameter at breast height, leaf area index, height and canopy spread are 22 cm, 2.4 m² m⁻², 18 m and 11 m², respectively.

Soil under the rubber tree monoculture 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 Mekong River (or Lancang River). Soil bulk density is 1.2 g cm⁻³ with an organic matter content of 25.9 g kg⁻¹ (0–20 cm) and a pH of 5.4 (Lu *et al.*, 2009).

This region has a strongly seasonal climate with two main air masses alternating during the year. Climatologically, the SW monsoon from the Indian Ocean delivers 80–90% of the annual rainfall without influence from the Pacific typhoons

during the rainy season (between May and October), whereas the southern edges of the subtropical jet streams dominate the climate during the dry season (between November and April) (Vogel *et al.*, 1995; Liu *et al.*, 2007). Climate records for the past 40 years show 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 30%). The mean annual rainfall is 1480 mm, of which most occurs between May and October and practically no rain fall between November and April (Liu *et al.*, 2007). During the pronounced dry season, high solar radiation associated with high temperature and low relative humidity lead to high vapour pressure deficit, increasing the evapotranspirative demand of the atmosphere (Ziegler *et al.*, 2009). During the late dry season, soil moisture under the rubber tree monoculture reaches close to permanent wilting point, and severe soil drought in subsoil occurs (Vogel *et al.*, 1995). Hence, rubber trees in this region are every year subjected to prolonged periods of both soil and atmospheric drought stress during the dry season (Chen and Cao, 2008).

Water, plant and soil sampling

Water samples for isotope analysis were collected from rainwater, groundwater, plant xylem water and soil water. Samples for main rain events were routinely collected at a weather station (about 1.0 km from the study site) from September 2008 to August 2009, except the period from early November 2008 to late March 2009 where no rain events occurred. In total, 29 rain samples in the rainy season and in the late dry season were collected. Samples of rainwater were collected immediately from a rain gauge after rain ceased or in the early morning when rain fell overnight. Groundwater samples were collected with a pump from an active well less than 0.2 km from the study site within the same catchment. Groundwater level is generally more than 10 m below the ground surface at the site throughout the year (Yang, personal communication). Samples of rainwater and groundwater were stored in 10 ml screw-cap glass vials, wrapped in Parafilm and frozen for later analysis.

Two field sites on a southeast-facing hillside were selected for the plant and soil investigation: one at the upslope and one at the downslope. Distance between the two sites is about 200 m in length along the slope. Samples of plant and soil for isotope analysis were collected separately in the late rainy season (18 October 2008), the late dry season (29 March 2009) and the early rainy season (11 May 2009). At midday of each sampling date, plant xylem samples were obtained from each of three selected rubber trees per sampling site. 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. All green stem tissues were removed from these stems to avoid contamination of xylem water by isotopically enriched water (Ehleringer *et al.*, 2000; Querejeta *et al.*, 2007). Samples of superficial lateral roots were also obtained from each of the selected trees at each site during the early rainy season collection to compare root water and stem isotopes. Lateral root tissues (2–3 mm diameter) just below the soil surface (0–5 cm) were harvested. This methodology, assuming that evaporative processes have not affected plant water in non-photosynthetic tissue, permits the analysis of water taken up by roots (Dawson and Pate, 1996; Corbin *et al.*, 2005). Upon collection, the clipped stem and root samples were immediately placed in 10-ml glass vials, tightly closed with Teflon-sealed caps, wrapped in Parafilm, kept in a cooler with ice in the field and kept frozen (–20 °C) in the laboratory prior to water extraction.

Soil samples were collected with a 4-cm-diameter hand-operated bucket auger. On each sampling date, three locations within the planting line between the selected trees were randomly chosen per sampling site (upslope and downslope). Soil samples were collected from depths of 5, 10, 20, 30, 50, 70, 90, 110 and 130 cm at each location. Gravimetric SWC (%) was determined from the sample weight loss by drying all samples at 105 °C for 48 h. At the same time, the water isotopic gradient in the soil profile was sampled by taking sequential soil cores. Soil samples were stored as previously described for root and stem samples.

Midday leaf water potentials (Ψ_{md}) of three to five leaves taken from sunny positions on each sampling tree were measured using a PSYPRO Water Potential System with Wescor C-52 Sample Chambers (WESCOR INC., Logan, USA). Measurements were performed *in situ* immediately after cutting between 12:30 and 13:30. Ψ_{md} were measured separately in the late rainy season (10 October 2008), the late dry season (12 March 2009) and the early rainy season (1 May 2009). For Ψ_{md} and isotope determinations, the same rubber trees were sampled repeatedly on successive dates. In order to explore rooting spatial distribution, root density was also determined along three trenches at each site in the early rainy season (1 May 2009). Each trench was located in the planting line between two trees, with a 0.6 m × 1.0 m cross section. Trenches were only dug to a depth of 1.3 m because this procedure was extremely labour demanding, but we observed that a few coarse roots still extended into deeper layers. Trench sidewalls were smoothed and roots exposed by removing 3–5 mm of soil. Roots within spatially registered 10 cm × 10 cm grid cells along trench faces were counted, and the characters of coarse and fine roots were recorded (Midwood *et al.*, 1998; Rouspard *et al.*, 1999).

Water was extracted from plant stem and soil samples by using a cryogenic vacuum distillation line (Ehleringer *et al.*, 2000). The $\delta^{18}\text{O}$ values of the water samples were

determined using the carbon dioxide equilibration method outlined by Dugan *et al.* (1985). The ^{18}O contents of the stem water, soil water, rainwater and groundwater were measured using a Finnigan MAT Delta V advantage isotope ratio mass spectrometer (Thermo Finnigan, USA) at Stable Isotope Ratio Mass Spectrometer Facility, Chinese Academy of Forestry, with accuracy of $\pm 0.2\%$ for $\delta^{18}\text{O}$. Isotope ratios of oxygen are expressed in ‰ relative to V-SMOW (Ehleringer *et al.*, 2000).

Water source modelling

Two methods were used to evaluate root water uptake of rubber trees. One was the direct inference approach (Jackson *et al.*, 1995; Asbjornsen *et al.*, 2008). In this approach, the isotopic composition of plant stem water was assumed to be an integrated measure of the water in the soil horizons from which plants actively took up water (Ehleringer *et al.*, 2000; McCole and Stern, 2007). Comparisons of the isotopic compositions of stem water and potential sources of soil water at different depths were made to identify the most probable sources of water uptake. This approach assumes that there are no other possible water sources other than soil water (Asbjornsen *et al.*, 2008). An important limitation to this approach occurs when the isotopic gradient is not asymptotic and irregularities in the isotopic gradient in the soil profile occur. As contributions of water from different water sources could account for the same stem water isotope values, actual plant water sources may be misinterpreted on the basis only of the direct inference approach (Asbjornsen *et al.*, 2008). Therefore, isotope values of potential water sources (different soil layer) and those for stem water were also analysed with the IsoSource mixing model to evaluate relative contribution of each soil depth to stem water (Phillips and Gregg, 2003). This method was based on multi-source mass balance. For the soil and plant stem sampled at the same time, according to the mass balance of soil water and its isotopes, the possible proportions of each soil layer (f_1, f_2, \dots, f_i) can be determined by their isotopic signature ($\delta X_1, \delta X_2, \dots, \delta X_i$) and the mixture (δX_p , i.e. the isotope value of plant stem water):

$$\delta X_p = f_1 \delta X_1 + f_2 \delta X_2 + \dots + f_i \delta X_i \quad (1)$$

$$f_1 + f_2 + \dots + f_i = 1 \quad (2)$$

In this analysis, 0–130 cm soil profile in each site was subdivided into three depth intervals (<30 cm, 30–70 cm and >70 cm) to facilitate comparison of water sources for rubber trees following the approach suggested by Phillips *et al.* (2005) and Asbjornsen *et al.* (2008). Although these depths are uneven, they were selected on the basis of rooting depth inspection and analysis of soil water isotope profile (Asbjornsen *et al.*, 2008). The isotopic composition for each

depth interval was determined using the water-content-weighted mean approach (Snyder and Williams, 2003; McCole and Stern, 2007). The isotopic compositions of the three depths and those for stem water were then analysed with the model to evaluate the relative contribution of each soil depth to stem water. This model does not give a discrete solution, but calculates a range of possible solutions. Hence, average source proportions were presented along with the range of minimum and maximum proportions (Phillips *et al.*, 2005). Uncertainty level was set at 0.2% in the model calculation following Asbjornsen *et al.* (2008) and Nie *et al.* (2012).

In our analysis, groundwater was not assumed to be a water source available to rubber trees because groundwater level is generally more than 10 m below the ground surface at the study site throughout the year (Yang, personal communication).

Statistical analysis

All statistical analyses were conducted using the program SPSS 13.0 (SPSS Inc., Chicago, USA). Seasonal patterns of stem water $\delta^{18}\text{O}$ were investigated with an analysis of variance (ANOVA) with season and site as fixed effects. ANOVA was also used to examine the main and interactive effects of season, site and soil depth on soil water $\delta^{18}\text{O}$ and SWC. Significant differences ($P < 0.05$) between sites within sampling dates and leaf water potential, root distribution and stem water $\delta^{18}\text{O}$ were detected using one-way ANOVA followed by a post hoc Fisher's least significant difference test.

RESULTS

Seasonal rainfall and isotopic composition

Total rainfall during the dry season (November 2008–April 2009) was 160.6 mm, 16% lower than the long-term mean (191.0 mm) for this period, but included a pronounced dry spell of more than 4 months without rainfall (Figure 1). This severe drought was terminated by a rain event (18.6 mm) on 26 March 2009, 3 days prior to the plant sampling date during the late dry season. Rainwater $\delta^{18}\text{O}$ varied with season during the study period (ranging from -15.10% to -0.52%), with the isotope values more depleted in the rainy season than in the dry season ($P < 0.001$). $\delta^{18}\text{O}$ values for groundwater varied only slightly over the year, ranging from -9.59% in the rainy season to -8.16% in the dry season.

Soil moisture and isotopic composition

Soil water content underwent pronounced seasonal changes down to 130 cm depth at both sites, with lowest values in the late dry season and highest values in the late rainy season (Figure 2). Soil moisture also decreased with depth at the

VERTICAL PATTERNS OF SOIL WATER ACQUISITION BY RUBBER TREES

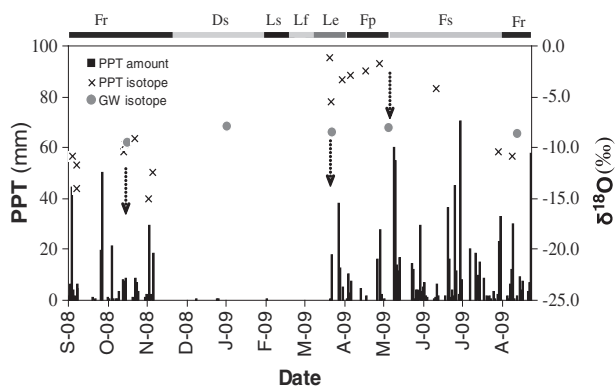


Figure 1. Distribution of daily precipitation (PPT) and variation of $\delta^{18}\text{O}$ values for event rainwater and groundwater (GW) during the rainy/dry season cycle (2008–2009). The stippled bars at the top of the panel are phenophases for rubber trees, i.e. Fr representing fruit ripening, Ds dormant stage, Ls leaf shedding, Lf leaf flushing, Le leaf expansion, Fp flowering phase and Fs fruit setting. Vertical arrows indicate sampling dates.

two sites during the late dry season and the early rainy season. Generally, shallow soil at the downslope exhibited a better water condition compared with the upslope. The difference in SWC between the two sites was significantly higher during the late rainy season in the top 30 cm and

below 70 cm of the soil [$P < 0.05$; Figure 2(a)], whereas similar SWC was observed at all depths in the soil profile during the early rainy season [$P > 0.05$; Figure 2(c)]. In the late dry season, a significant difference was found in the top 20 cm and depths between 50 and 70 cm of the soil [$P < 0.05$; Figure 2(b)]. Season, site and depth had significant effects on SWC ($P < 0.001$; Table I). The interactions of season \times depth, site \times depth and season \times site \times depth were also significant ($P < 0.001$), but season \times site was not ($F_{2,108} = 1.555$, $P = 0.216$).

Soil water $\delta^{18}\text{O}$ values differed significantly among seasons, sites and depths ($P < 0.001$; Table I). With the exception of $\delta^{18}\text{O}$ in the rainy season, soil water was isotopically enriched near the surface (varying between -5‰ and -1‰) relative to deeper soil (varying between -11‰ and -8‰) at every sampling period. In the late rainy season [Figure 3(a) and (b)], the relatively depleted $\delta^{18}\text{O}$ values near the surface (around -8‰) likely resulted from the combined effects of recent inputs of isotopically depleted monsoon rainfall (around -10‰ ; Figure 1), 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

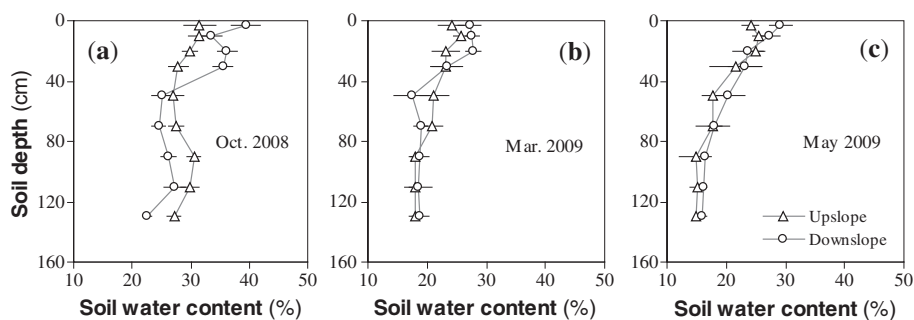


Figure 2. Vertical profiles of soil water content at (a) the late rainy season, (b) late dry season and (c) early rainy season at the upslope and downslope positions.

Table I. Results of analysis of variance showing differences in soil water content and soil water $\delta^{18}\text{O}$ over season, site and depth in the experimental catchment.

Source	df	SWC (%)			$\delta^{18}\text{O}$ (‰)		
		MS	F	P	MS	F	P
Season	2	705.818	253.054	<0.001	106.433	1300.180	<0.001
Site	1	28.125	10.084	0.002	45.739	558.747	<0.001
Depth	8	332.614	119.251	<0.001	44.908	548.587	<0.001
Season \times site	2	4.339	1.555	0.216	1.072	13.101	<0.001
Season \times depth	16	9.853	3.532	<0.001	16.988	207.519	<0.001
Site \times depth	8	46.443	16.651	<0.001	0.685	8.372	<0.001
Season \times site \times depth	16	32.638	11.702	<0.001	1.948	23.796	<0.001
Error	108	2.789	—	—	0.082	—	—

SWC, soil water content; MS, Mean square.

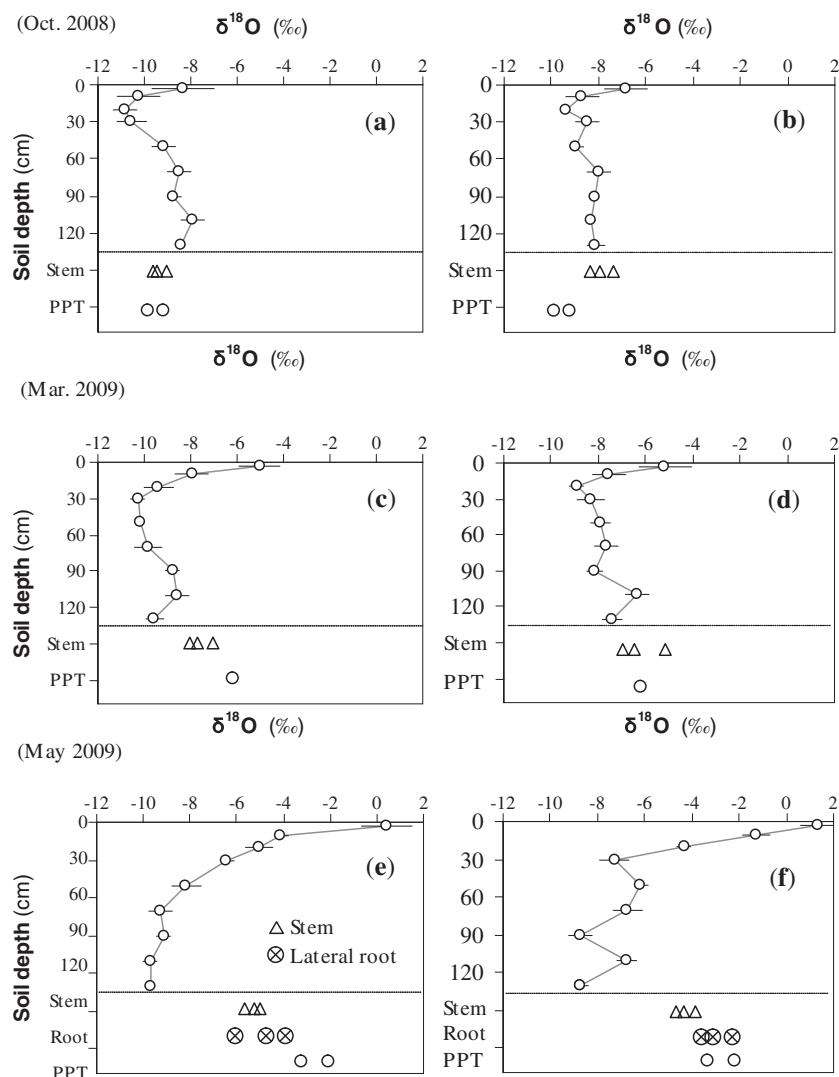


Figure 3. Vertical profiles of soil water $\delta^{18}\text{O}$ at the downslope (left) and upslope (right) positions. $\delta^{18}\text{O}$ values for stem water and antecedent event rainwater (PPT) are shown at the bottom of each panel. Note that $\delta^{18}\text{O}$ values for superficial lateral roots in the early rainy season (May 2009) are also shown.

establishment of a stable isotope gradient in the soil profile through strong evaporative enrichment (Barnes and Turner, 1998). For all the sampling events, soil water was isotopically more enriched at the upslope relative to the downslope site ($P < 0.05$).

Isotopic value of stem water and depth of water uptake

Pooling all data, stem water isotope ratios were significantly affected by season and site ($P < 0.001$; Table II) but not by their interaction ($F_{2, 12} = 1.079$, $P = 0.371$). There was a consistent seasonal trend in stem $\delta^{18}\text{O}$ values at both sampling sites, with the lowest values (around -9‰) from the late rainy season and highest values (around -4‰) from the early rainy season (Figure 3). This trend reflects the rainfall history of the region (Figure 1) and differences between topographic positions of the two sites (see

Table II. Results of analysis of variance showing differences in stem water $\delta^{18}\text{O}$ over season and site in the experimental catchment.

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>
Season	2	18.161	100.996	<0.001
Site	1	5.014	27.883	<0.001
Season \times site	2	0.194	1.079	0.371
Error	12	0.180	—	—

MS, Mean square.

Discussion section in the succeeding text). For each sampling date, stem $\delta^{18}\text{O}$ values at the downslope were significantly lower than those at the upslope ($P < 0.05$; Figures 3 and 4). The more enriched stem $\delta^{18}\text{O}$ values along with the more enriched shallow soil $\delta^{18}\text{O}$ values and the

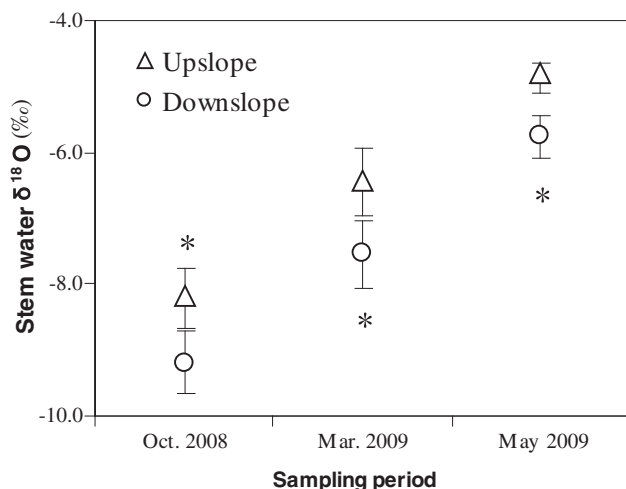


Figure 4. Mean stem water $\delta^{18}\text{O}$ (± 1 standard error, $n=3$) for the rubbers at the upslope and downslope positions. * indicates significant difference between upslope and downslope ($P < 0.05$).

more superficial lateral roots present at the upslope (Figure 5) suggest that rubber trees tapped more shallow sources of soil water at the upslope than at the downslope. Also, plant stem water $\delta^{18}\text{O}$ matched those of the top soil (<30 cm) fairly well in each sampling event (Figure 3), reflecting the response of these trees to the most recent rainfall.

In the late rainy season at the downslope, isotopic data from stems matched soil water values at the top 20 cm depth and around 70 and 90 cm depth; whereas at the upslope, they were similar to the values at the top 10 cm and below depths of 70 cm, suggesting that dominant source of water uptake from these soil layers had occurred [Figure 3(a) and (b)]. As the pronounced dry period (i.e. late dry season) progressed, main depth of plant water uptake at both sites shifted to deeper levels in the soil profiles (around 90 and 120 cm at

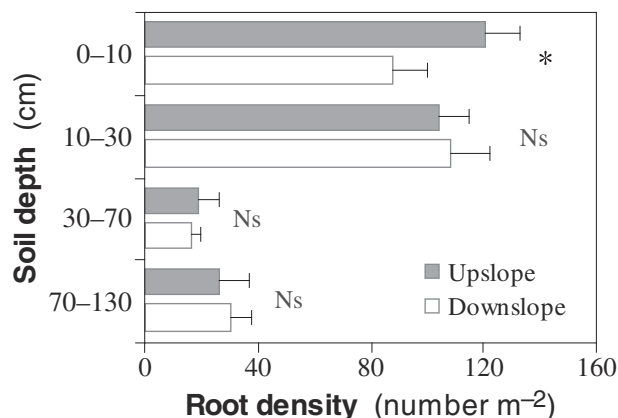


Figure 5. Mean root density (± 1 standard error, $n=6$) with depth for rubbers at the upslope and downslope positions. * indicates significant difference ($P < 0.05$), and Ns no significant ($P > 0.05$) between upslope and downslope.

the downslope and below 110 cm at the upslope) and those remained unchanged in the shallow soil [Figure 3(c) and (d)]. The lack of change at shallow depths likely resulted from an 18.6-mm rain event (Figure 1), which markedly increased plant water at that layer. This was in agreement with our rooting distribution data (Figure 5), which showed that extensive lateral roots were maintained in the top soil (<30 cm) and could opportunistically exploit shallow soil water recharged by the most recent rainfall event over the dry season.

Significant rainfall occurred as the early rainy season [Figure 3(e) and (f)] progressed into the early monsoon period, and plant water uptake appeared to be restricted to a relatively shallow layer (around 30 cm) under well-watered conditions compared with the previous late dry season. Similarly, depth of water uptake by lateral roots was also restricted to the shallow soil layers, as shown by their $\delta^{18}\text{O}$ signatures, which were similar to or slightly higher than those of stem waters.

Similar to the aforementioned analysis, the IsoSource model also predicted that rubber trees greatly relied their water (varying between 49% and 71%) on the shallow soil water (<30 cm) and extracted only a small fraction of water (varying between 14% and 30%) from the deep soil (>70 cm) at both sites (Table III), suggesting that rubber trees are functionally dimorphically rooted and may have had access to both shallower and deeper water sources throughout the year. In the late dry season and early rainy season, after a long-lasting drought, soil moisture in the middle layers (30–70 cm) was gradually depleted by plant root extraction [Figure 2(b)], and consequently, water utilization from these layers decreased sharply at both sites (<15%) (Table III).

Plant water potential

For each sampling event, the midday leaf water potentials (Ψ_{md}) between the two sites were not significantly different ($P > 0.05$), although Ψ_{md} at the downslope (-1.28 MPa) was slightly higher than at the upslope (-1.46 MPa) during the late dry season (Figure 6). Compared with the late rainy season, a subsequently dry spell caused Ψ_{md} to drop slightly at both sites, but the difference was not significant ($P > 0.05$). Also, no significant difference in Ψ_{md} values was found between the early rainy season and the late dry season at either site.

DISCUSSION

Inspection of the rooting system under our rubber tree monoculture is well consistent with observations from a mature rubber tree stand in the same area (Guardiola-Claramonte *et al.*, 2008). Similarly, Philip *et al.* (1996), Devakumar *et al.* (1999) and George *et al.* (2009) pointed

Table III. Proportions of feasible water sources (%) for rubber trees growing at the downslope and upslope positions in the experimental catchment in the late rainy season (October 2008), late dry season (March 2009) and early rainy season (May 2009).

Water source ^a	October 2008		March 2009		May 2009	
	Downslope	Upslope	Downslope	Upslope	Downslope	Upslope
<30 cm	49 (17–62)	52 (32–77)	66 (45–89)	71 (51–91)	65 (15–82)	69 (21–87)
30–70 cm	21 (0–41)	20 (0–35)	13 (0–21)	10 (1–27)	19 (0–35)	17 (0–33)
>70 cm	30 (10–54)	28 (4–36)	21 (1–38)	19 (3–29)	16 (0–31)	14 (2–27)

^a Average source proportions calculated by the IsoSource mixing model (Phillips and Gregg, 2003) are shown along with the range of minimum and maximum proportions (in parentheses).

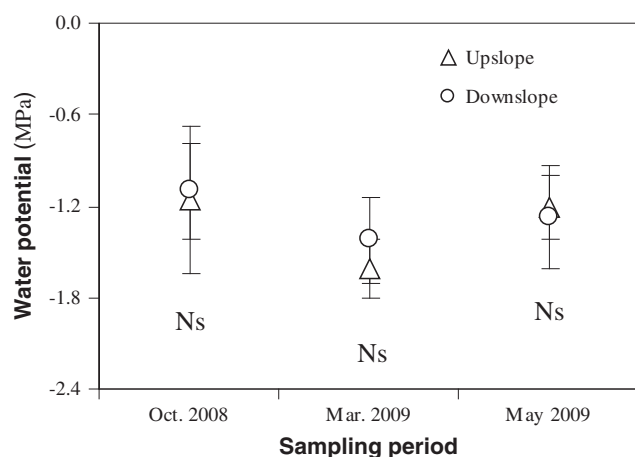


Figure 6. Mean midday leaf water potential (± 1 standard error, $n=9$) for the rubbers at the upslope and downslope positions. Ns indicates no significant difference between upslope and downslope ($P > 0.05$).

out that rubber tree is a surface feeder, and in mature rubber trees, about 55–86% of the total active roots are confined to the top 0–20 cm of soil. The higher concentration of feeder roots near the soil surface may be attributed to the accumulation of organic matter through litter decomposition at the surface layer (Philip *et al.*, 1996), and the sharp decline in root density with increasing depths signals that increased inter-tree competition would occur near the surface of the soil (George *et al.*, 2009). In addition, some differences in the root distribution pattern were evident between the upslope and downslope positions in our stand, with more superficial lateral roots present at the upslope ($P < 0.05$) where the soil water condition was relatively poor compared with the downslope (Figures 2 and 5). This difference might be because of the greater production of lateral roots in response to drought (Gasteller and Vartanin, 1995). The greater development of lateral roots in soil layers with relatively poor water condition may be an adaptation of trees for more efficient water/nutrients absorption (Sternberg *et al.*, 2004). A similar pattern of rubber tree rooting distribution was also observed in a severely drought-prone area on the west coast of India (Devakumar *et al.*, 1999).

Because most of the roots are within the top 30 cm of the soil zone (Figure 5), rubber trees can take advantage of rapidly infiltrating water supplied by rainfall several days prior to sampling (recent rainfall event), as demonstrated by soil and stem water isotope signatures (Figure 3). Soil and stem water $\delta^{18}\text{O}$ data along with rooting distributional patterns revealed that rubber trees acquired their water mostly from the top 30 cm and less from below 70 cm of the soil profile during the late rainy season when soil water was plentiful. During the late dry season, as the moisture in the middle soil layers was gradually depleted by root extraction and water availability decreased (Figure 2), the depth of water uptake shifted to deeper soil levels. However, the proportion of water uptake from the shallow soil layer (<30 cm) also increased markedly after an occasional rainfall event in the late dry season and the early rainy season (Table III), indicating significant plasticity in sources of water uptake in this dimorphic-rooted species. A previous observation in the same area also found that rubber tree is efficient in using the available water in the root zone (Guardiola-Claramonte *et al.*, 2010). Querejeta *et al.* (2006) found a similar result in a seasonally dry tropical area in Mexico. Several other studies conducted in seasonally dry tropical forests have concluded that trees depend mostly on water stored within the shallow soil/subsoil profile during the dry season (Drake and Franks, 2003; Andrade *et al.*, 2005; Romero-Saltos *et al.*, 2005; 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. This results from the functionally dimorphic root system in rubber trees that acquires water predominantly from shallow soil where the highest density of roots is present but can also use deeper soil water, as shown elsewhere for other tree species (Donovan and Ehleringer, 1994; Dawson and Pate, 1996; Lin *et al.*, 1996; Meinzer *et al.*, 1999; Ewe and Sternberg, 2002; Darrouzet-Nardi *et al.*, 2006).

During the early rainy season, stem $\delta^{18}\text{O}$ increased significantly and also revealed absorption of the most recent rainfall, as shown by the $\delta^{18}\text{O}$ signatures in the superficial lateral roots [Figure 3(e) and (f)]. The general similarity in

stem and lateral root $\delta^{18}\text{O}$ values indicated that the superficial lateral roots were completely involved in the main supply of shallow soil water to the canopy, as found in other studies (Thorburn and Ehleringer, 1995; Dawson and Pate, 1996; Roupsard *et al.*, 1999). Clearly, greater lateral spread or higher density of roots in the shallow soil layer can compensate for limited ability to access water stored within the deeper soil zone in rubber trees.

Results from the IsoSource model revealed that the brevideciduous rubber trees at the two sites extracted more water from the shallow soil layers and less water from the deep soil layers throughout the year (Table III). This is inconsistent with our initial assumption that rubber trees obtain water primarily from greater depths in the soil profile but consistent with the results of some other studies (Andrade *et al.*, 2005; Romero-Saltos *et al.*, 2005; Nippert and Knapp, 2007). The ability to tap deep soil water sources has been noted by Jackson *et al.* (1999), Stratton *et al.* (2000) and Querejeta *et al.* (2007), who found that deciduous tree species tended to rely on deeper water sources in a Brazilian Cerrado savanna, in a Hawaiian dry tropical forest and in a tropical agroforest vegetation in northern Yucatan.

In contrast to our hypothesis, the upslope and downslope rubber trees utilized similar proportions of deep soil water but with significantly higher water uptake from the shallow soil layer (<30 cm) over the year, especially at the upslope position in the late dry season (71%) (Table III). This is quite consistent with the rooting inspection, showing that a greater proportion of superficial roots were present at the upslope and a few deeply penetrating roots present in the deeper layers (Figure 5), which could enable the utilization of more water from the top layer and less water from the deeper, as mentioned previously. This water-use strategy appears to be very important for species growing in water-limited environments, especially in seasonally dry tropical regions (Querejeta *et al.*, 2007).

The rubber tree, as a non-native brevideciduous species (i. e. short synchronous shedding, and subsequent leaf flushing and expanding during the late dry season) in this area, is dormant from mid-November to late February and retains its foliage until mid-February, when leaves are shed within about two weeks (Figure 1). Bud break and new leaf growth generally start in early March, several weeks before the arrival of the first monsoon rain. As pointed out by Elliott *et al.* (2006), rubber tree flushing is independent of climate and is primarily associated with photoperiodic induction (increase in day length) and the availability of subsurface water. However, leaf flushing during the dry season implies that this species must have access to sufficient reserves of water for subsequent leaf expansion and shoot growth (Elliott *et al.*, 2006). In addition, while shedding reduces transpiration, simultaneous root water uptake increases stem water potential that is needed for subsequent bud breaking

and leaf flushing (Guardiola-Claramonte *et al.*, 2008). Our data showed that in the late dry season, when rubber tree leaves expanded rapidly, the moisture in the middle soil layers were greatly depleted by root extraction [Figure 2(b)], coinciding with the changes in rubber tree phenology (Figure 1). Also, the occasional rainfall event was opportunistically exploited by the shallow lateral roots to meet the greater water requirements during the dry period (through the late dry season to the early rainy season) (Table III; Figure 3). Similarly, Guardiola-Claramonte *et al.* (2008) used extensive field observations of root zone soil moisture in rubber trees in this area to show that a sudden increase of water uptake takes place from mid-March through the end of March, quite consistent with the aforementioned findings. A study in northern India showed an increase in girth perimeter several weeks before the first rainfall (Chandrashekar *et al.*, 1998), possibly indicating rehydration of the rubber tree from sufficient water uptake, associated with bud breaking.

Despite the long-lasting dry season, rubber trees avoided severe drought stress in our study stand. This lack of drought stress was probably related to the functionally dimorphic rooting system (Stratton *et al.*, 2000) of the rubber trees and the drought-tolerant clone as well (Devakumar *et al.*, 1999; Chen and Cao, 2008). On sunny days, Ψ_{md} was relatively stable and did not decrease significantly during the late dry season (Figure 6). Such a pattern indicates isohydric behaviour, which maintains leaf hydration above a critical Ψ_{md} value by means of stomatal closure (West *et al.*, 2007; Isarangkool Na Ayutthaya *et al.*, 2011). Isarangkool Na Ayutthaya *et al.* (2011) also found that this isohydric behaviour in rubber trees appears to be consistent with the observation of tight regulation of transpiration when evaporative demand is high. Within our sampling dates, Ψ_{md} ranged between -0.6 and -1.7 MPa, in agreement with results of previous studies from a dry subhumid area of India (Chandrashekar *et al.*, 1998; Devakumar *et al.*, 1999) and from a drought-prone area of northeast Thailand (Isarangkool Na Ayutthaya *et al.*, 2011) but was slightly higher than the values they measured. The drought response of the clone measured here, PB86, may differ from that used in the studies mentioned previously (RRIM 600), and a comparative study revealed significant clonal variability of water response to soil and atmospheric drought (Chandrashekar *et al.*, 1998).

Other studies in this area found that water use by rubber trees was high in the dry season (Guardiola-Claramonte *et al.*, 2008, 2010). This comparatively high water use suggests a potential threat to the dry-season stream flows and groundwater resources in landscapes where vast expanses of native forest have been converted to rubber plantations. In fact, results from 15 years of paired catchment observations and 1 year eddy covariance estimates in this study area have already demonstrated that more water evapotranspired from the rubber plantation than from the

rainforest (Tan *et al.*, 2011). Similarly, hydrological model simulations made by Guardiola-Claramonte *et al.* (2010) also found that the conversion of forest cover to rubber tree in this area depleted water storage from the subsurface soil during the dry season, increased water loss through evapotranspiration and reduced discharge. Both these results and ours shown here lend support to the idea that rubber trees act as 'water pumps'. But this idea still remains to be confirmed because our data and those from others are quite limited or just based on small basin-scale studies. Further study involving a more intense sampling scheme to determine seasonal patterns in water use (including rubber tree transpiration and water source), as well as more detailed analysis of plant-water cycling processes and water balance, is required to better understand the hydrological and ecological consequences of extensive land-cover conversion to rubber tree plantation at a larger scale.

CONCLUSIONS

Non-native rubber trees, a brevideciduous spring flushing species, greatly relied their water (varying between 49% and 71%) on the shallow soil water (<30 cm) and extracted only a small fraction of water (varying between 14% and 30%) from the deep soil layers (>70 cm). During the late dry season, as the soil moisture in the middle layers (30–70 cm) was gradually depleted, water utilization from these layers decreased sharply (<15%). However, the proportion of water uptake from the shallow soil layer increased markedly after the most recent rainfall during the late dry season and the early rainy season (varying between 65% and 71%), indicating significant plasticity in sources of water uptake in this dimorphic-rooted species. This ability to opportunistically take up a large proportion of shallow soil water after rainfall is likely the key feature enabling rubber trees to thrive through the period of greatest water demand. These results suggest that rubber trees in this area are able to adjust the allocation of resources and thus acclimate to the spatiotemporal changes to water conditions in the soil profile.

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