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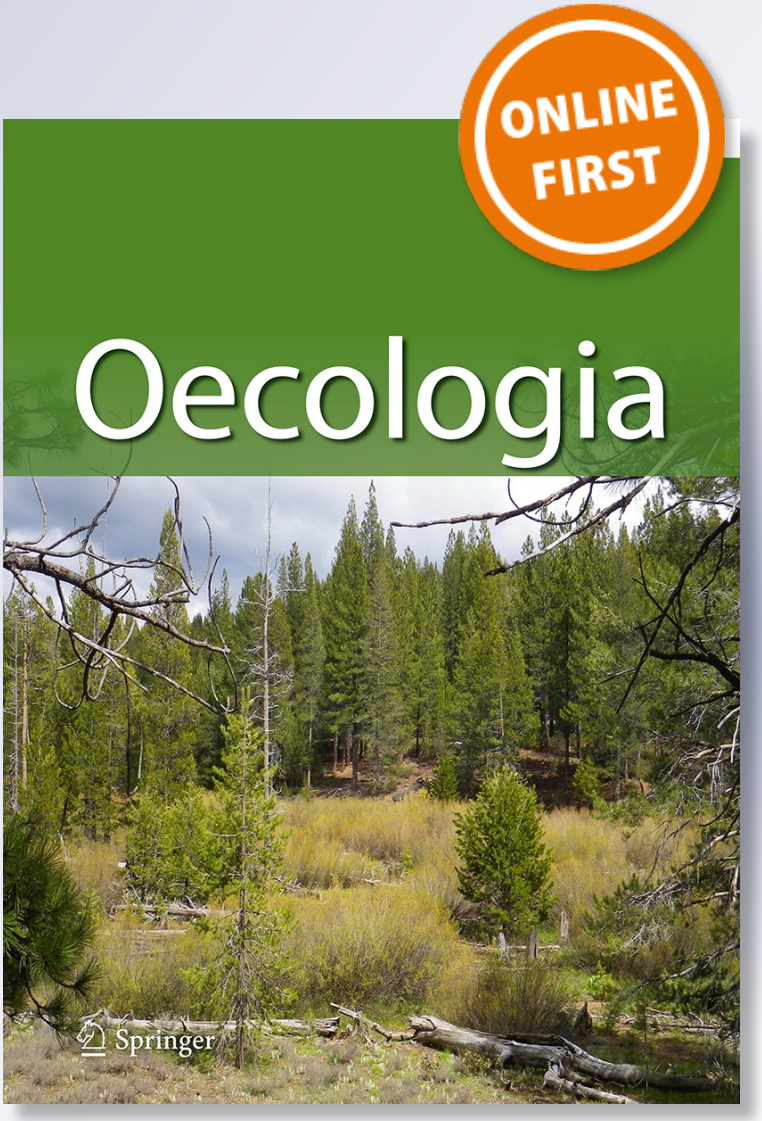
Oecologia

ISSN 0029-8549

Oecologia
DOI 10.1007/s00442-013-2724-6



Springer

Oecologia
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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Depth of soil water uptake by tropical rainforest trees during dry periods: does tree dimension matter?

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Received: 13 December 2012 / Accepted: 25 June 2013

Abstract Though the root biomass of tropical rainforest trees is concentrated in the upper soil layers, soil water uptake by deep roots has been shown to contribute to tree transpiration. A precise evaluation of the relationship between tree dimensions and depth of water uptake would be useful in tree-based modelling approaches designed to anticipate the response of tropical rainforest ecosystems to future changes in environmental conditions. We used an innovative dual-isotope labelling approach (deuterium in surface soil and oxygen at 120-cm depth) coupled with a modelling approach to investigate the role of tree dimensions in soil water uptake in a tropical rainforest exposed to seasonal drought. We studied 65 trees of varying diameter and height and with a wide range of predawn leaf water potential (Ψ_{pd}) values. We confirmed that about half of the studied trees relied on soil water below 100-cm depth during dry periods. Ψ_{pd} was negatively correlated with depth of water extraction and can be taken as a rough proxy of this depth. Some trees showed considerable plasticity in their depth of water uptake, exhibiting an efficient adaptive strategy for water and nutrient resource acquisition. We did not find a strong relationship between tree dimensions and depth of water uptake. While tall trees preferentially extract water from layers below 100-cm depth, shorter trees show broad variations in mean depth of water uptake. This precludes the use of tree dimensions to parameterize functional models.

Keywords Deuterium · Oxygen · Soil water · Tropical rainforest · Root

Communicated by Gerardo Avalos.

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Introduction

In tropical rainforest regions, despite high annual rainfall, large seasonal variations in rainfall occur which lead to periods of water shortage for the plant communities (Malhi and Wright 2004). In the context of global environmental change, questions such as how tropical rainforest species will adapt to future constraints on soil water availability (Wang et al. 2011) and how seasonal variations in rainfall will influence tropical rainforest ecosystem functioning have been central to a large range of recent research studies. At the ecosystem level, seasonal variations in soil volumetric water content (VWC) have been shown to induce changes in carbon, water and energy fluxes in Amazonian, South Asian and African tropical rainforest ecosystems (Da Rocha et al. 2004; Goulden et al. 2004; Hutyra et al. 2007; Bonal et al. 2008; Merbold et al. 2009; Zhang et al. 2010). These variations arise from the impact of environmental

Published online: 14 July 2013

conditions on processes at both the soil and the tree level. Particularly, at the tree level, seasonal variations in VWC usually result in a decrease in leaf photosynthesis and transpiration of tropical rainforest species (Bonal et al. 2000a; Cao 2000; Engelbrecht and Kursar 2003; Baraloto et al. 2007; Stahl et al. 2013). Nevertheless, this general trend actually hides distinct tree-specific response patterns. Indeed, in all the above-mentioned experiments, a non-negligible percentage of the trees did not display significant changes in leaf gas exchange or water status during dry periods. For instance, in French Guiana, Stahl et al. (2013) studied the physiological response of tropical rainforest canopy tree leaves to seasonal reductions in relative extractable water and found that 20 % of the canopy trees were unaffected by the strong decrease in soil water availability.

Why is it that some tropical rainforest tree species do not experience a strong reduction in leaf water status during dry periods? First, large differences in drought tolerance among tropical tree species have been described (Baraloto et al. 2007; Poorter and Markesteijn 2008). Drought avoidance may occur through drought-adaptive mechanisms such as stomatal regulation, osmotic regulation (Kozlowski and Pallardy 2002), regulation of proteins related to the water transfer among cells (synthesis in Chmura et al. 2011), or thanks to specific biophysical characteristics that allow more water transfer to take place in the soil–plant-atmosphere continuum (e.g. high hydraulic conductivity). Second, the ability of the fine root system of some trees to explore deep soil layers that remain wet even during dry periods could also explain these different response patterns (Oliveira et al. 2005; Markewitz et al. 2010). A few studies have attempted to evaluate the vertical distribution of root biomass in tropical rainforests (Nepstad et al. 1994; Carvalheiro and Nepstad 1996; Sternberg et al. 1998; Davidson et al. 2011). Root biomass usually displays an exponential decrease with depth with less than 10 % found below 100-cm depth, even though some roots have been known to reach soil layers below 10 m (Nepstad et al. 1994; Jackson et al. 1996; Davidson et al. 2011). However, root biomass vertical distribution does not perfectly reflect the depth at which trees extract water. Even though deep root biomass represents only a small part of total root biomass, such deep roots may actively contribute to tree transpiration in tropical rainforests (Romero-Saltos et al. 2005; Markewitz et al. 2010; Davidson et al. 2011).

The relationship between the depth of water uptake by tropical rainforest trees and tree dimensions is still being debated. Are large trees necessarily able to extract water from deeper layers than smaller ones? Romero-Saltos et al. (2005) pointed out that deep soil water might be accessible only to large-diameter trees. However, this conclusion contradicts Sternberg et al. (1998) who showed that roots from a wide range of tree diameter classes colonized both upper and deep soil layers. Furthermore, Meinzer et al. (1999) showed that during dry periods, small-diameter trees extract water from even deeper layers than large-diameter ones. A precise evaluation of the relationship between tree dimension and depth of water uptake would be very useful in tree-based modelling approaches that intend to describe the response of tropical rainforest ecosystems to future changes in environmental conditions.

In this study, we investigated the relationship between depth of water uptake and tree dimensions in a tropical rainforest in French Guiana submitted to large seasonal variations in rainfall. We addressed whether large trees necessarily develop deep roots and extract water from soil layers below 100-cm depth during dry periods while small-diameter, suppressed trees, only rely on shallow soil layers. We also tested whether predawn leaf water potential (Ψ_{pd}) of tropical rainforest trees could be used as a proxy of the mean depth of water uptake. Thanks to an innovative dual isotope labelling of oxygen and deuterium in water and a modelling approach, we investigated the depth of soil water uptake of 65 trees with a wide range of heights, diameters, positions in the canopy, and Ψ_{pd} values.

Materials and methods

Study site and plant material

This study was conducted near the Guyaflux eddy flux tower (Bonal et al. 2008) at the Paracou forest site in French Guiana, South America (5°16′54″N, 52°54′44″W). Mean annual rainfall at the study site is 3,041 mm (Gourlet-Fleury et al. 2004) and mean air temperature is around 25.7 °C. In French Guiana, the climate is affected by the north/south movements of the inter-tropical convergence zone which cause large seasonal variations in rainfall. In May and June, the region receives around 500–800 mm of rain per month whereas during the long dry season that extends from mid-August to mid-November, only 50–100 mm of rain falls per month (Bonal et al. 2008; Stahl et al. 2010).

At this site, soils are mostly nutrient-poor acrisols (FAO-ISRIC-ISSS, 1998) with pockets of sandy acrisols developed over a Precambrian metamorphic formation. Deep ferralitic, sandy-clay soils with free vertical drainage cover the summit of the hills in this area (approximately 45 m above sea level) and exhibit a reddish-brown clayey horizon with a micro-aggregated structure followed by a red clayey weathered horizon at a depth of less than 120 cm. Clay and sand content in the 100-cm-deep horizon on the upper parts of the hills is about 43 and 48 %, respectively (Bonal et al. 2008).

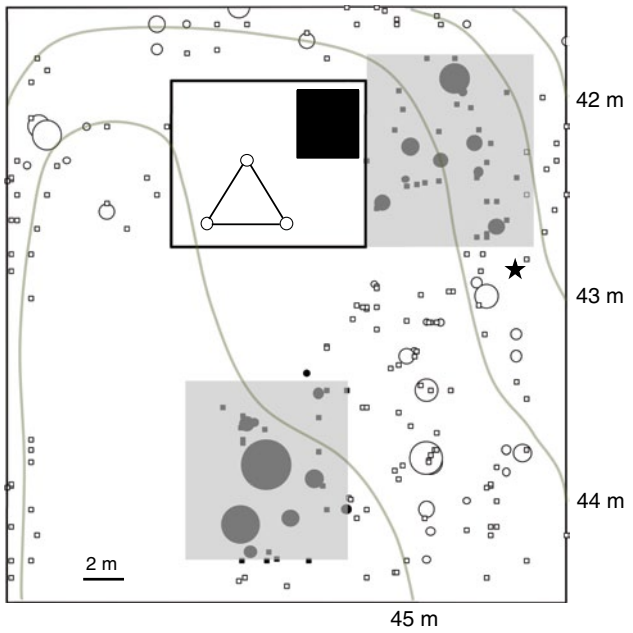

Fig. 1 Map of the study site. *Grey* areas indicate the two plots where the labelling experiment was conducted. *Black circles* correspond to the sampled trees and *white circles* correspond to the neighbouring trees in the vicinity of the labelling experiment. For the trees with a diameter at breast height above 10 cm, the size of the circle is proportional to its diameter at a scale 3 times that of the map. For smaller trees, the size of the square is fixed. The *star* represents the location where soil volumetric water content measurements were recorded. The *large triangle* represents the poles of the Guyaflux tower and the *black rectangle* represents the bungalow that houses the data loggers and electrical equipment. The *empty area* corresponds to the sandy access road to the tower. The *grey lines* represent isoclines

We delineated two plots (88 and 92 m^2) near the Guyaflux tower (Fig. 1) where we selected all the trees above 2 m high, for a total of 65 trees with a large range of diameters (1.3–79.9 cm) and heights (2.0–38.0 m). The trees were identified taxonomically and represent 47 different species. Only two species were represented by more than two trees. This study thus was not designed to test any species difference in the depth of water uptake, but only to describe the variability in the depth of the considered population. We also included in the study nine other trees that were located on the same hill, at least 15 m from the two plots (diameter 8.8–37.2 cm and height 10.0–33.0 m). These trees served as a control for the natural isotopic abundance of xylem water over the study period; we assumed that their lateral roots would not reach the plots (Sternberg et al. 2002). In each plot, we installed grid lines with strings on the ground every 1 m to delineate 1-m^2 subplots.

In the forest surrounding the study site, tree density averages 620 trees ha^{-1} and tree species richness is about 140 species ha^{-1} (diameter at breast height >10 cm). Mean tree height is 35 m, with emergent trees exceeding 40 m (Bonal et al. 2008).

Predawn leaf water potential

We used a Scholander-type pressure chamber (model 1000; PMS Instruments, Corvalis, OR) to measure Ψ_{pd} on one leaf per selected tree in the morning before labelling was conducted. Leaves were sampled between 6.00 and 7.00 a.m. in the upper part of the crown with clippers connected to extension loopers or by a qualified tree climber from our team. Precise Ψ_{pd} measurements could not be obtained for seven trees in the Myristicaceae and Sapotaceae because they have translucent latex which mixes with the xylem sap and exudates from the petiole when pressure is applied in the chamber.

Soil VWC

Soil VWC (m^3 m^{-3}) was measured at five depths (10, 20, 80, 160 and 260 cm) near the two plots (Fig. 1) with frequency domain sensors (CS616; Campbell Scientific, Logan, USA) set up in 2007. It was automatically recorded every 60 s by a data logger (CR23X; Campbell Scientific) and averaged every 30 min. Daily means were then calculated.

Labelling experiment

Oxygen labelling

Following the approach presented by Zapater et al. (2011), we injected a small amount of water with very high oxygen isotope composition ($\delta^{18}O$) at 120-cm depth. The roots located around this depth could thus take up the labelled water and the $\delta^{18}O$ of xylem water in the corresponding trees would increase. Two weeks before the labelling experiment, we dug 114 holes distributed over the two plots on the 1-m × 1-m grid. We were not able to dig holes at some locations on the grid because of surface roots, buttresses, or the presence of a trunk, and these locations were therefore either discarded or moved slightly. The holes were dug with a jackhammer equipped with a drill core (Cobra TT; Eijkelkamp, the Netherlands). The holes were 120-cm deep and 35 mm in diameter. In each hole, we buried a PVC tube (length = 120 cm, diameter = 35 mm) up to 105 cm, in order to leave a 15-cm-long space at the bottom of the hole (i.e. a volume of 0.25 l) to receive the labelled water. The free space at the bottom of the hole also helped to avoid possible contamination of the upper layers of soil by capillary action along the PVC tube.

Preliminary isotope analyses conducted on soil samples collected at this site in September 2010 over a 200-cm

depth profile showed that the natural abundance of oxygen in the soil water at the site was around −3.0 to −5.0 ‰. We therefore chose to inject a solution with $\delta^{18}O = 500$ ‰ as we suspected the diffusion of labelled water in these soils to be low. To prepare the labelled water, we mixed an $H_2^{18}O$-enriched solution (98.0 atom %, i.e. $\delta^{18}O = 2.44E + 07$ ‰; Cambridge Isotope laboratories, MA) with tap water from the laboratory in Kourou ($\delta^{18}O = -1.4$ ‰) with a 1:861.96 ratio. Further oxygen isotope analyses revealed that the isotope composition of the prepared solution was 456.4 ‰.

On 7 November 2010, between 8.00 and 10.00 a.m., we poured 125 ml of labelled water from a graduated test tube into each tube through a small funnel. In the evening of the same day, we inserted a thin stick down to the end of each tube to check that all the labelled water had drained down into the soil.

Deuterium labelling

Preliminary analyses conducted as for ^{18}O showed that the natural abundance of deuterium in the soil water at the site ranged between −45.0 and −20.0 ‰. Our objective was to bring a volume of highly labelled water ($\delta^2H \approx 10{,}000$ ‰) equivalent to 5 mm of rain to the upper soil layers. To prepare the labelled water (885 l), we mixed a highly concentrated deuterium solution (99.85 atom %, i.e. $\delta^2H = 4.27E + 09$ ‰; Cambridge Isotope laboratories) with tap water from the laboratory in Kourou (deuterium isotope composition $\delta^2H = -11.0$ ‰) in a 1-m^3 plastic tank, with a 1:635.13 ratio. Further isotope analyses revealed that the isotope composition of the prepared solution was 9,951.2 ‰ for deuterium and −1.4 ‰ for oxygen. Immediately after the oxygen-labelled water was injected (7 November 2010), we watered each 1-m^2 delineated subplot with a regular spray of 5 l of the prepared solution. Spraying was done after coarse litter had been raked up to ensure rapid percolation of the labelled water. The litter was raked back into place after spraying.

Soil sampling

In order to analyse the oxygen and deuterium isotope composition of soil water at different depths (down to 200-cm depth), we sampled soil cores ($n = 6$ cores per plot and per campaign) with a manual auger 4 days before labelling (C0; 3 November 2010), 3 days after labelling (C1; 10 November) and 10 days after labelling (C2; 17 November). Each core was split into nine segments (20 cm or 30 cm long each) that were put into plastic bags, carefully sealed, and taken to the laboratory in an icebox with freeze packs where they were stored at 2 °C to reduce the risk of evaporation. Great care was taken to rinse the auger and the operator's hands with tap water and to carefully dry them after each segment had been collected.

Branch sampling

At each date when soil samples were collected, a 100- to 300-cm-long branch of each tree (diameter 10–30 mm) was sampled in the upper part of the tree crown with clippers connected to extension loopers or by a qualified tree climber. At the base of each collected branch, a piece of branch of about 7 cm in length was collected. Bark tissue was immediately removed in order to avoid any contamination with phloem sap. The samples were placed in plastic tubes, sealed with parafilm, and taken to the laboratory in an icebox with freeze packs where they were stored at 2 °C. Great care was taken to rinse the clippers and the hands of the operators with tap water after handling each sample. Branches were sampled at about the same time of the day (8.00–11.00 a.m.) for a given tree for the three sampling campaigns in order to avoid any bias related to the daily variation in tree transpiration.

Isotope analyses

Soil and plant samples were shipped to the INRA stable isotope facility (PTEF) in Nancy, France. Water was extracted through cold trapping with a cryogenic vacuum distillation system. The oxygen and deuterium isotope composition was determined on separate samples of 0.3–0.4 µl of water extracted from the soil (soil water) and the branch samples (xylem water). The measurements were taken with an IsoPrime isotope ratio mass spectrometer (GV Instruments, Manchester) coupled to a Pyr-OH liquid autosampler (Eurovector, Milan). Measurement precision for $\delta^{18}O$ and δ^2H, respectively, was better than 0.3 and 0.7 ‰ ($n = 50$). For both $\delta^{18}O$ and δ^2H, two measurements were taken for each water sample and only the second one was retained. The isotopic ratios were expressed relative to the international standard Vienna-standard mean ocean water (V-SMOW) as:

$$\delta = 1{,}000 \times \frac{(R_s - R_{std})}{R_{std}}, \quad (1)$$

where R_s is the sample ratio of heavy to light isotope and R_{std} refers to the V-SMOW standard.

Estimation of mean depth of water uptake

Values of δ^2H in soil and xylem water were used to estimate the mean depth of water uptake by the root system of a tree at a given date in accordance with the model developed by Romero-Saltos et al. (2005). This model

assumes that, at a given time, trees extract water from a 50-cm vertical segment of soil and the amount of water extracted within this segment follows a normal distribution. The length of 50 cm was selected by Romero-Saltos et al. (2005) based on data from the literature. Furthermore, Romero-Saltos et al. (2005) conducted simulations with different lengths and found no effect on the final estimations of the depth of water uptake of each studied trees. We also tested different lengths and confirm Romero et al.'s (2005) findings (data not shown). In addition, we improved the model by including a truncated normal distribution to take into account the upper and lower limits of the considered soil layer (i.e. 0–200 cm) as follows:

$$f(x, \mu, \sigma) = \frac{\mathrm{Cn}}{\sqrt{2\pi}\,\sigma} \exp\left\{-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2\right\}, \quad (2)$$

where *C*n is a normalization constant defined as:

$$\mathrm{Cn} = 1/\int_{-200}^{0} \frac{1}{\sqrt{2\pi\sigma}} \exp\left\{-\frac{1}{2}\left(\frac{x-\mu}{2}\right)^2 \mathrm{d}x\right\} \quad (3)$$

where $f(x, \mu, \sigma)$ is the proportion of water extracted at depth x, μ is the mean depth of water uptake, and σ is the SD from this normal distribution. A normal distribution of the depth of water uptake means that 99.7 % of the water extracted by the trees comes from a vertical segment of soil that is approximately $\mu \pm 3\sigma$ cm long. Because we assumed that a tree takes up water from a 50-cm segment of soil, σ here thus equals 8.33 cm. This model is also based on the assumption that, according to mass balance principles, the deuterium signature in the xylem water is equal to the sum of the deuterium signatures of the soil water absorbed at different depths:

$$\delta^2 H_{\mathrm{e}}^{\mathrm{xylem}} = \sum_{i=1}^{m} (n_i \times \delta^2 H_i^{\mathrm{soil}}), \quad (4)$$

where $\delta^2 H_{\mathrm{e}}^{\mathrm{xylem}}$ is the estimated deuterium isotopic composition of the xylem water, m is the maximum depth analysed, and $\delta^2 H_i^{\mathrm{soil}}$ is the average isotopic composition of soil water at the $_i$th depth. For a given deuterium profile in the soil, there are m possible $\delta^2 H_{\mathrm{e}}^{\mathrm{xylem}}$ values, each with a corresponding mean depth of water uptake (μ). For each considered depth along the 50-cm segment, the model calculates a $\delta^2 H_{\mathrm{e}}^{\mathrm{xylem}}$ value based on the $\delta^2 H_i^{\mathrm{soil}}$ profile values and compares it with the measured δ^2H of the xylem water for each tree. The best match (optimize function in R-program) between the estimated and measured δ^2H gives the estimated mean depth at which the tree preferentially extracts water, again considering a truncated normal distribution around this mean depth.

Data analyses

A change in the δ^{18}O of xylem water was attributed to oxygen labelling when: (1) the difference between values of δ^{18}O of xylem water before labelling (C0) and after labelling (C1 and C2) was higher than 1 ‰, and (2) the δ^{18}O of xylem water was higher than −4 ‰ in C1 or C2. These threshold values were selected according to the precision of the isotopic analyses and the values obtained before labelling. Similarly, taking into account the deuterium isotope composition (δ^2H) of soil and xylem water before labelling, variations in δ^2H in xylem water were attributed to deuterium labelling when: (1) the difference in δ^2H of xylem water between C0 and C1 or C2 was higher than 20 ‰, and (2) the δ^2H of xylem water was higher than −15 ‰ in C1 or C2.

A *t*-test was used to compare the soil water δ^2H and δ^{18}O values of each campaign for every soil layer and to compare the xylem water δ^2H and δ^{18}O values among campaigns for the nine trees outside the two plots. Linear models were used to test any relationship between mean depth of water uptake and tree dimension (height, diameter) or Ψ_{pd}. A change in the depth of water uptake between two dates was considered to have occurred when the difference in depth between the two dates was greater than the length of the soil segment in the normal distribution (i.e. superior to 50 cm). The Bonferroni outlier test was used to detect any tree that would deviate markedly from other trees of the population in the depth/leaf water potential relationship. All statistical tests were conducted with the R software (R Development Core Team 2010).

It should be noted that because ^{18}O-labelled water was injected into the soil at a depth of 120 cm on a point basis, the absence of an increase in the δ^{18}O of xylem water as compared to baseline values (i.e. before labelling) does not necessarily mean that the root systems of the studied trees were not exploring soil layers below this 120-cm depth. Indeed, they may well have been extracting water at around 120-cm depth or even deeper, but through parts of the root system which were not located in the vicinity of the injection points. However, an increase in the δ^{18}O of xylem water clearly indicates that one part at least of the root system of a given tree was located at or below 120-cm depth and that the tree significantly used labelled water for its transpiration.

Results

The 2010 dry season in French Guiana was very marked. Between 1 September and 7 November 2010 (date of labelling)—a period of 68 days—only 25.6 mm of rain was

measured at the study site and only 2.2 mm of rain was recorded during the 10 days prior to labelling (Fig. 2). A strong decrease in soil VWC was observed between September and November in the upper soil layers (down to 0.10 m^3 m^{-3}), whereas VWC at 260-cm depth remained above 0.28 m^3 m^{-3} (Fig. 2). Deuterium-labelled irrigation (5 mm) induced a negligible increase in VWC at 10-cm depth (i.e. 0.01 m^3 m^{-3}) and had no effect for all the other soil layers.

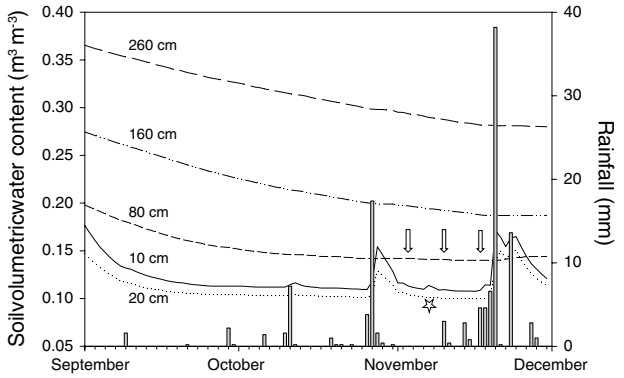

Fig. 2 Variations in daily cumulated rainfall (*bars*) and in soil volumetric water content (VWC) at 10-cm (*solid line*), 20-cm (*dotted line*), 80-cm (*short dashed line*), 160-cm (*dash-dot line*) and 260-cm (*long dashed line*) depth, before and after the labelling experiment. The *vertical arrows* indicate sampling dates and the *star* the day of isotope labelling

Before labelling (C0), the natural abundance of ^2H in soil water had a clear vertical stratification with a strong decrease from −17.8 to −37.0 ‰ between the soil surface and the 90-cm depth (Fig. 3a). Below 90-cm depth, there was a slight increase and δ^2H reached −28.8 ‰ at 190-cm depth. A similar stratification was observed for $\delta^{18}O$, with upper soil layer values around −1.9 ‰ and minimum values around −4.9 ‰ (Fig. 3c).

Labelling induced a strong increase in soil water δ^2H from the surface to 70-cm depth up to 600.0 ‰ in C1 and C2 (Fig. 3b). There were no significant differences in soil water δ^2H in C1 and C2 for any given depth, except at 50 cm where C2 values were slightly higher than C1 values ($P < 0.001$). Below 70 cm, we observed an increase in soil water δ^2H of about 20.0 ‰ between C0 and C1 or C2 ($P < 0.001$).

Soil water $\delta^{18}O$ values in C1 and C2 at a given depth did not show significant differences with C0, except at 190-cm depth (Fig. 3d). This result may seem surprising since ^{18}O-labelled water was injected into the tubes at 120-cm depth (see "Materials and methods"). Nevertheless, the absence of a large increase in $\delta^{18}O$ directly below 120 cm can be explained by the fact that the soil cores made at C1 and C2 to characterize the vertical profile of soil water

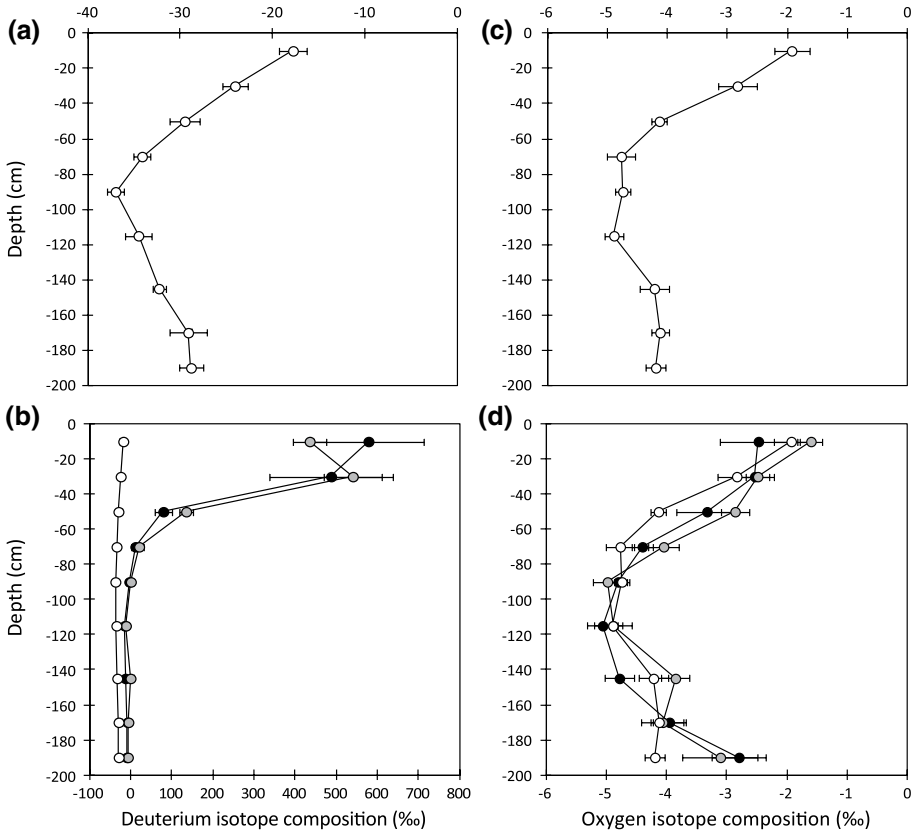

Fig. 3 *Left* vertical profile of soil water deuterium isotope composition (δ^2H; ‰). **a** Prior to labelling (C0; i.e. natural abundance, *open circles*, *long dashed line*), **b** prior to labelling (C0; *open circles*), 3 days after labelling (C1; *black circles*) and 10 days after labelling (C2; *grey circles*). *Right* The same vertical profiles for soil water oxygen isotope composition ($\delta^{18}O$; ‰). Data are mean ± SE (*horizontal bars*) of six cores per sampling date. Note: C0 values are given above with a smaller range on the *x*-axis for graphical clarity

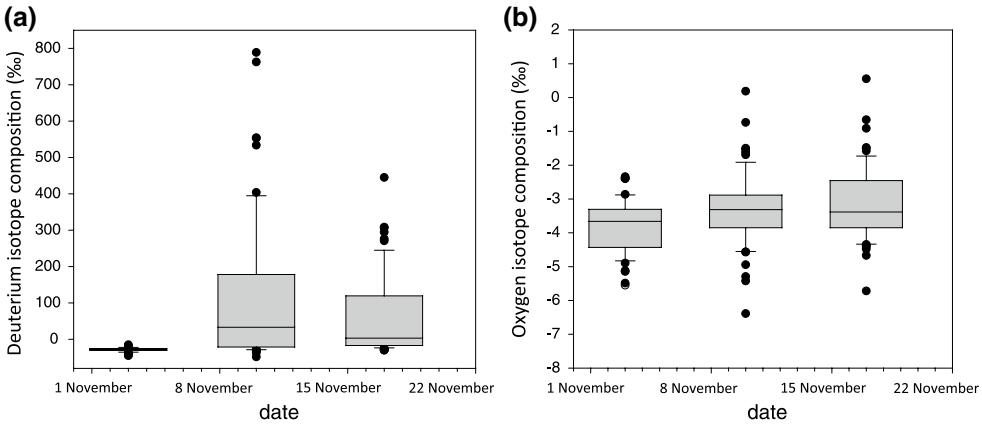

Fig. 4 **a** *Box plot* of xylem water deuterium isotope composition (δ^2H; ‰) and **b** *box plot* of xylem water oxygen isotope composition (δ^{18}O; ‰), for the three campaigns (C0 = 7 November, C1 = 10 November, C2 = 17 November 2010). *C0* corresponds to the natural abundance. $n = 65$ trees for C0, C1 and C2, respectively. For abbreviations, see Fig. 3

δ^{18}O were located in the middle of the squares defined by the 100-cm grid set up for the tubes—about 70 cm from the injection tubes. Obviously, the lateral drainage of the δ^{18}O-labelled water was not strong enough to show any increase in the δ^{18}O of the soil samples that we collected in the cores at C1 and C2. Nevertheless, the fact that some trees did show a clear increase in the δ^{18}O of xylem water (see below) confirms the presence of ^{18}O-labelled water in the soil.

The natural δ^2H of xylem water ranged between −15.4 and −44.9 ‰ (Fig. 4a). After labelling, a total of 49 trees (75.0 %) showed a strong increase in xylem water δ^2H in one campaign at least: up to 811.6 ‰ in C1 and 472.2 ‰ in C2 (Fig. 4a). Twenty-one (32.3 %) and 23 (35.4 %) trees in C1 and C2, respectively, showed no clear change in δ^2H compared with values in C0. Trees that were selected outside the two plots showed no significant change in xylem water δ^2H from C0 to C1 or C2 (mean values of −35.5 ± 2.3, −30.6 ± 1.7 and −31.4 ± 1.9 ‰ in C0, C1 and C2, respectively, $P > 0.50$).

Natural δ^{18}O of xylem water ranged between −2.3 and −5.6 ‰ (Fig. 4b). After injection, 18 (27.7 %) and 23 (35.4 %) trees in C1 and C2, respectively, showed a clear increase in δ^{18}O. Not all trees displayed an increase at both dates but a total of 30 trees (46.2 %) showed an increase in δ^{18}O in one campaign at least. Among those 30 trees, 37 % displayed a depth of soil water uptake below 100-cm depth, as estimated by the ^{2}H model.

Trees that were selected outside the two plots showed no change in δ^{18}O from C0 to C1 or C2 (mean values of −3.7 ± 0.2, −3.3 ± 0.5 and −3.4 ± 0.3 ‰ in C0, C1 and C2, respectively, $P > 0.50$).

The distribution of the mean depth of water uptake obtained with the δ^2H model showed two peaks at 50–70 and 110 cm in depth for both C1 and C2 (Fig. 5). About 41.5 and 52.3 % of the trees in C1 and C2, respectively, displayed a mean depth of water uptake below 100-cm depth (Fig. 5). Nine trees out of 65 (14 %) showed a clear change in estimated mean depth of water uptake between two dates (i.e. more than 50 cm) (Fig. 6).

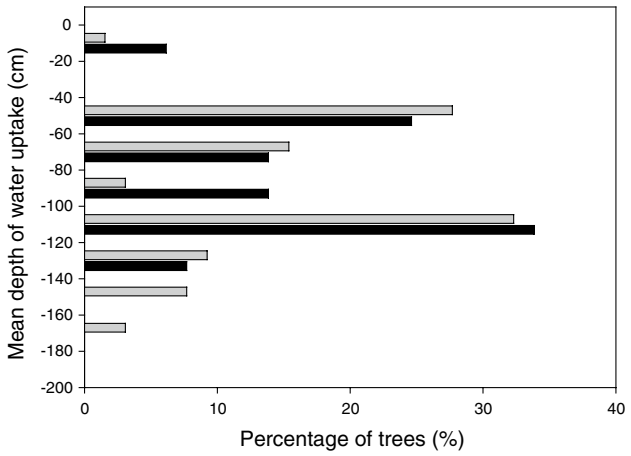

Fig. 5 Percentage of the number of trees in the different classes of mean depth of soil water uptake in C1 (*black bars*) and C2 (*grey bars*). For abbreviations, see Fig. 3

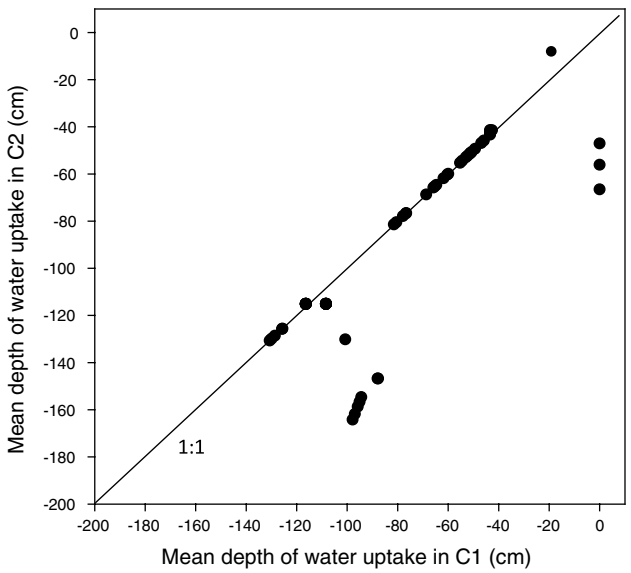

Fig. 6 Relationship between the estimated mean depth of water uptake in C2 and C1. $n = 65$ trees. For abbreviations, see Fig. 3

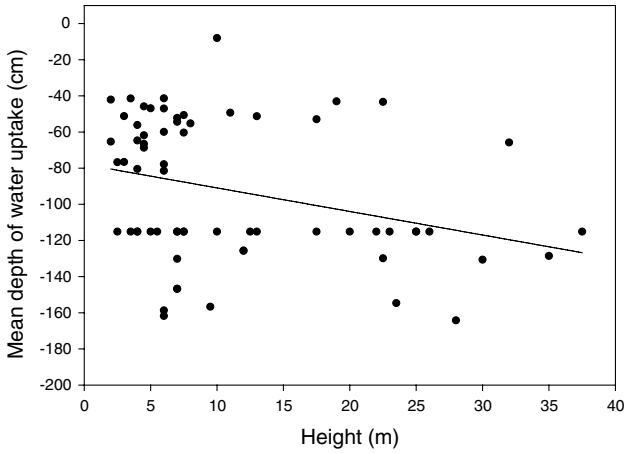

Fig. 7 Relationship between the estimated mean depth of water uptake and the height of the sampled trees in C2. The *solid line* represents the linear regression line ($R^2 = 0.08$, $P = 0.02$, $n = 65$ trees)

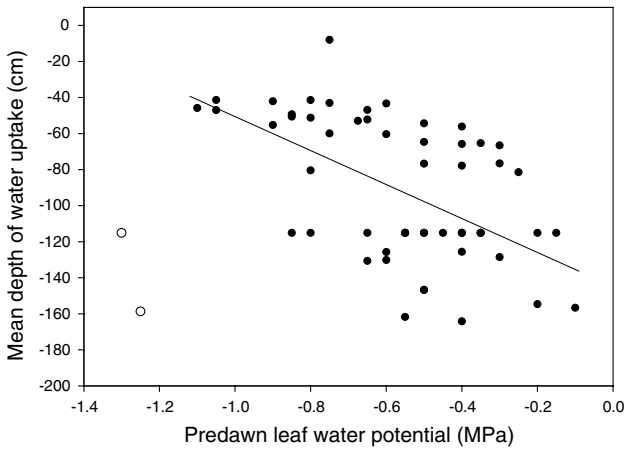

Fig. 8 Relationship between the estimated mean depth of water uptake and predawn leaf water potential in C2. The *solid line* represents the linear regression line ($R^2 = 0.30$, $P < 0.001$, $n = 63$ trees) when the two trees which deviate markedly from the others (*open circle*) were excluded

There was a significant negative relationship between the mean depth of water uptake and tree height for both campaigns ($P < 0.001$, $R^2 = 0.15$; $P = 0.012$, $R^2 = 0.10$ for C1 and C2, respectively; Fig. 7). We also found a significant negative relationship between the mean depth of water uptake and tree diameter for both campaigns ($P = 0.004$, $R^2 = 0.12$; $P = 0.036$, $R^2 = 0.07$ for C1 and C2, respectively) (data not shown).

There was a significant negative relationship between the mean depth of water uptake and Ψ_{pd} for both campaigns ($P = 0.02$, $R^2 = 0.10$; $P = 0.007$, $R^2 = 0.13$ for C1 and C2, respectively) (Fig. 8). For these relationships, the Bonferroni test detected one outlier tree, and one tree, although not statistically detected by this test, also appeared to deviate from the other samples. When these two trees were removed from the analyses, relationships became more significant for both campaigns ($P < 0.001$, $R^2 = 0.19$; $P < 0.001$, $R^2 = 0.30$ for C1 and C2, respectively) (Fig. 8).

Discussion

The seasonal variations in rainfall in 2010 resulted in severe soil drought conditions at the soil surface from the end of October to the end of November (Fig. 2). Studies conducted at this site have demonstrated that such severe soil water restrictions result in strong limitations to secondary growth (Wagner et al. 2011) and/or leaf gas exchange of canopy trees (Bonal et al. 2000a; Stahl et al. 2013). Even during such severe drought conditions, VWC was nearly 0.15 $m^3\ m^{-3}$ at around 100-cm depth and remained as high as 0.28 $m^3\ m^{-3}$ at 260-cm depth, i.e. much higher than VWC thresholds below which tree functioning and growth are hindered (Wagner et al. 2012).

The role of deep roots

Our study confirms the active role that roots below 100-cm depth play in water uptake during dry periods for the studied population of tropical rainforest trees. Three independent elements allow us to confirm this result. First, a large range of Ψ_{pd} values were observed among trees at the end of the dry season (−0.1 to −1.3 MPa), with values below -0.5 MPa for about 34.0 % of the trees. This variability in Ψ_{pd} is consistent with previous studies conducted at the site (Bonal et al. 2000a; Stahl et al. 2011, 2013) but is greater than the one found in Para, Brazil (Fisher et al. 2006). Ψ_{pd} of a given tree can be used as a proxy for the water potential of the soil where the root system of this tree is actively extracting water (Améglio et al. 1999). Therefore, the variability in Ψ_{pd} we observed clearly confirms that the root systems of these trees were exposed to highly contrasted soil water conditions along the soil vertical profile. Second, the huge increase in δ^2H of soil water in the upper soil layers after labelling (Fig. 3) was not necessarily associated with an increase in δ^2H of xylem water. Twenty-five percent of the trees showed a mean estimated depth of water uptake below 100-cm depth (Fig. 5). This shows that transpiration of these trees mainly relied on wet layers below 100-cm depth (Fig. 2). Third, 46.1 % of the trees clearly absorbed $\delta^{18}O$-labelled water at least once. Such an increase indicates that these trees were extracting water at or below 120-cm depth. The increase in xylem water $\delta^{18}O$ for these trees was low, but nevertheless remained within the range observed by Zapater et al. (2011) in a similar soil ^{18}O labelling experiment conducted in a temperate forest.

Our results are consistent with the general assumption that water uptake by roots below 100-cm depth represents an efficient adaptation to seasonal variations in rainfall for tropical rainforest trees in Amazonia (Nepstad et al. 1994; Moreira et al. 2000; Romero-Saltos et al. 2005; Markewitz et al. 2010). This result helps to explain why the ecosystem surrounding these plots displays a reduction in ecosystem productivity (Bonal et al. 2008) and transpiration (D. Bonal, personal observation) during severe dry seasons of only about 20 %. Trees which develop a deep root system strategy will likely be able to delay the negative effects of drought on plant water status in the context of upcoming climatic changes.

Relationship between depth of water uptake and tree dimension

One major objective of this study was to assess the relationship between tree dimensions and depth of water uptake. Even though a significant negative relationship between tree height (or diameter) and mean depth of water uptake was observed (Fig. 7), this relationship explains only a very small part of the wide variability observed (15 and 10 % in C1 and C2, respectively). In fact, the mean depth of water uptake for the small trees included the whole soil profile, while the tall trees (> 25 m) preferentially extracted water from 60- to 120-cm depth (Fig. 7). Furthermore, both tall and short trees extracted $\delta^{18}O$-labelled water in this experiment. Our results differ from those of Romero-Saltos et al. (2005) who concluded that only large trees access deep soil layers; and from those of Meinzer et al. (1999) who suggested a negative relationship between depth of water uptake and tree diameter. The following elements might explain these contradictions. First, our study was designed to directly address this issue: our sample size (65 trees) was much larger and covered a broader range of dimensions (2.0–38.0 m in height and 1.3–79.9 cm in diameter) than previous studies. Second, the discrepancy between this study and Meinzer et al. (1999) may actually arise from the methodology used and the depth of the soil layers they investigated. Meinzer et al. (1999) inferred depth of soil water uptake with the natural abundance of ^{2}H in xylem water and in soil water down to a depth of 100 cm. However, since this study, it has been demonstrated that using the natural abundance of ^{2}H or ^{18}O in tropical rainforest soils can lead to the misinterpretation of the depth of water uptake by trees (Bonal et al. 2000b; Moreira et al. 2000). Indeed, while vertical profiles of $\delta^{2}H$ or $\delta^{18}O$ down to 100-cm depth usually display log-shaped curves, they can actually show a C- or S-shaped form when a deeper soil profile is considered. Such complex vertical gradients arise because of seasonal variations in evaporation and in the isotope signature of rainfall (Bonal et al. 2000b; Moreira et al. 2000). Xylem water $\delta^{18}O$ or $\delta^{2}H$ values can then actually match soil water $\delta^{18}O$ or $\delta^{2}H$ values not only from the upper soil layers, but also from deeper layers. The absence of a strong relationship between tree dimensions and depth of water uptake prevents us from proposing any generalisations that could be used in modelling approaches to simulate the influence of soil water conditions on tropical rainforest ecosystem functioning (e.g. Williams et al. 1998).

Plasticity in depth of water uptake

One unexpected observation in our study was the temporal variability in the $\delta^{2}H$ of xylem water for nine trees after labelling, independent of dimension, revealing large differences from one date to another in the mean depth at which the trees extracted water (Fig. 6). Soil $\delta^{2}H$ values did not differ between C1 and C2 at any given depth and cannot explain the differences in $\delta^{2}H$ of xylem water between the two dates. Romero-Saltos et al. (2005) suggested that stimulation of new root production following labelling could explain this pattern. However, in our experiment, there was no change in VWC after labelling below 10-cm depth. This effectively eliminates the root production hypothesis since root production and turnover are strongly dependent on VWC levels (Yavitt and Wright 2001). Only a change in the preferential mean depth of water uptake between the two dates can explain the observed pattern. These results suggest strong plasticity and a profitable, dynamic, soil water and nutrient use strategy. Strong vertical gradients in nutrient levels exist in tropical rainforest ecosystems (Jobbagy and Jackson 2001). In order to efficiently acquire these nutrients, trees develop a dense root mat in the upper soil layers. Nevertheless, these trees seem to also be able to quickly change the depth at which they preferentially extract water during dry periods, in order to adapt to the changing soil water conditions. Trees with such root systems can also take advantage of the rare rain events during the dry season and the first heavy rains at the beginning of the wet season by acquiring water and nutrients from the upper soil layers.

Relationship between depth of water uptake and leaf water potential

We found a negative relationship between the mean depth of water uptake and Ψ_{pd} (Fig. 8). To our knowledge, such a comparison in a tropical rainforest had never been made before. This result showed that trees with a deeper depth of water uptake were able to maintain high Ψ_{pd} values during the dry season whereas Ψ_{pd} values of trees that rely only on upper soil layers decreased by at least 1.0 MPa. Highly negative Ψ_{pd} values during dry periods have been shown to increase the vulnerability of vessels to embolism

(Sobrado 1997) and to induce leaf gas exchange regulation for tropical rainforest tree species (Huc et al. 1994; Bonal et al. 2000a; Engelbrecht et al. 2002; Stahl et al. 2013). The observed relationship confirmed the adaptive advantage for trees with active roots below 100-cm depth to support seasonal variations in VWC. Nevertheless, values were widely dispersed along this relationship and we therefore conclude that Ψ_{pd} values during the dry season can only be used as a rough estimator of the mean depth of soil water extraction in tropical rainforest ecosystems. Two trees appeared to deviate strongly from the other trees (Fig. 8). No clear explanations are apparent: a total absence of transpiration at that time of the year could have occurred, with no water—labelled or not—actually being extracted from the soil. However, the two trees did have leaves and phenology could not explain such a lack of transpiration; a complete stomatal closure following severe soil drought could have induced such a mechanism. Further leaf gas exchange measurements are needed to confirm this hypothesis.

In conclusion, our study has confirmed that about half of the studied trees in this tropical rainforest ecosystem rely on the wet soil layers below 100-cm depth for transpiration during dry periods. Even if tropical rainforest trees tend to concentrate most of their root biomass in the upper soil layers to optimize nutrient acquisition, many of them also are able to access soil layers that remain wet during the dry periods. We confirmed that trees that use soil water below 100-cm depth display high Ψ_{pd} values during the dry season. Extracting water from these layers allows them to delay the time when regulation of carbon and water leaf gas exchange occurs during seasonal dry periods. There was no strong relationship between tree dimension (diameter or height) and depth of water uptake. While tall trees preferentially extracted water from layers below 100-cm depth, the shorter trees showed a broad range of mean depths of water uptake. This precludes the use of dimensions to parameterize tree-based functional models that intend to anticipate the response of tropical rainforest ecosystems to future changes in environmental conditions. The exploration of both deep and shallow soils in the dry season allows certain trees to adapt to seasonal variations in water and nutrient availability and might thus give them an adaptive advantage in the context of climate change. Further research is now needed to demonstrate whether these trees really benefit from this ability and display fewer seasonal variations in secondary growth patterns than other trees.

Acknowledgments We are grateful to J. Cazal, J.-Y. Goret, F. Kwasie, A. Etienne and B. Leudet for their field assistance in collecting leaves and soil samples. We thank P. Petronelli and J. Engel for the taxonomic identifications and C. Hossann for the water extraction work. We thank the handling editor and two anonymous reviewers for their comments on a previous version of this manuscript. This study was part of the GUYAFLUX project funded by the French Ministry of Research, INRA, and the CNES, in the framework of the PO-Feder Région Guyane, and was partially funded by an Investissement d'Avenir grant of the ANR (CEBA: ANR-10-LABEX-0025).

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