

Water acquisition patterns of two wet tropical canopy tree species of French Guiana as inferred from $H_2^{18}O$ extraction profiles

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Abstract – We inferred water acquisition patterns of two major tropical rainforest canopy tree species, during wet and dry seasons in different soil drainage conditions, based on the natural abundance of ^{18}O in soil and xylem water and on descriptions of the vertical extension of root systems. Vertical ^{18}O patterns in the soil were not monotonic and spatially distinct soil layers displayed similar ^{18}O values. Therefore, vertical patterns of water extraction could only be interpreted by combining the isotopic data with observed root and soil moisture vertical distributions. On sites with deep vertical drainage (DVD), *Eperua falcata* was able to absorb water down to at least –3.0 m depth, whereas *Dicorynia guianensis* depended solely on superficial layers. On sites with superficial lateral drainage (SLD), the rooting system of both species was less deep, but *Eperua falcata* was still able to extract water around –2.0 m depth. Despite these distinct patterns, there was no effect of seasonal soil drought on leaf water status. In terms of adaptation to seasonal soil drought, the strategy of *Eperua falcata* might be advantageous under occasional severe soil moisture stress.

$H_2^{18}O$ / rainforest canopy tree / water acquisition / *Eperua falcata* / *Dicorynia guianensis* / water-use efficiency

Résumé – Stratégies d'acquisition de l'eau de deux espèces majeures de la forêt tropicale humide guyanaise estimées par les profils d'extraction de $H_2^{18}O$. Nous avons estimé la distribution verticale de l'acquisition de l'eau chez deux espèces abondantes de la strate arborée supérieure en forêt tropicale humide, en saison sèche et en saison des pluies, pour des sols qui diffèrent par le type de drainage. Nous avons combiné une approche basée sur les mesures d'abondance naturelle en ^{18}O de l'eau dans le sol et dans l'aubier, et une approche basée sur la description de l'extension verticale du système racinaire des arbres. Les variations de $\delta^{18}O$ en fonction de la profondeur ne sont pas monotones, des valeurs similaires de $\delta^{18}O$ sont observées pour plusieurs horizons de profondeurs distinctes. L'interprétation des profils verticaux d'extraction d'eau n'est possible qu'en combinant les données isotopiques et les données relatives aux profils de prospection racinaire et de variations saisonnières d'humidité du sol. Sur le site à drainage vertical libre (DVD), *Eperua falcata* est capable d'absorber de l'eau jusqu'à 3.0 m de profondeur au moins, alors que l'alimentation en eau de *Dicorynia guianensis* repose essentiellement sur les horizons supérieurs. Sur le site à drainage superficiel et latéral (SLD), le système racinaire des deux espèces est moins profond, mais *Eperua falcata* puise tout de même de l'eau jusqu'à –2.0 m de profondeur. Malgré ces différences de profondeur d'extraction de l'eau, l'état hydrique des arbres est maintenu constant en saison sèche et en saison des pluies. En termes d'adaptation à la sécheresse du sol, la stratégie d'*Eperua falcata* pourrait présenter des avantages lors de sécheresses exceptionnelles.

$H_2^{18}O$ / forêt tropicale humide / acquisition de l'eau / WUE / *Eperua falcata* / *Dicorynia guianensis*

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1. INTRODUCTION

In recent years, a non-destructive methodology based on the assessment of natural abundance of stable oxygen (^{18}O) or hydrogen (^2H) isotopes in water has been used to assess the differential uptake and use of water sources among plants in different ecosystems [13, 14, 15, 16, 17, 22, 31, 36, 43]. This methodology is based on the fact that (1) soil water extraction by roots does not induce isotopic fractionation of either oxygen or hydrogen isotopes of water [2, 44, 45] and (2) gradients in oxygen or hydrogen isotope composition ($\delta^{18}\text{O}$ or $\delta^2\text{H}$) of soil water with soil depth may arise from seasonal variations in rainfall isotope signature [11, 12] and from the isotope fractionation that occurs during surface soil water evaporation (see review in [16]). Therefore, by comparing instantaneous $\delta^{18}\text{O}$ or $\delta^2\text{H}$ of xylem sap water with that of soil water, it is possible to interpolate a mean soil depth where roots extract water.

This methodology has been widely applied in dry or arid ecosystems [17, 22, 36, 43], but reports on the use of this method to infer water sources used by trees in dry tropical [31] or wet tropical [3, 19] forest remain scarce. The infrequent use of such an approach in the wet tropics might be associated with the weakness or absence of strong differences in seasonal isotopic signature of rainfall water and with the weak atmospheric evaporative demand in the understorey [3, 21]. However, Jackson et al. [31] found a strong gradient in $\delta^2\text{H}$ from surface down to 1.0 m depth in a lowland tropical forest in Panama and were then able to show that trees differing in leaf phenology also differed in their depth of water extraction. Therefore, this methodology appears as potentially useful for inferring differences in soil water extraction among wet tropical canopy tree species.

Tropical canopy rainforest tree species have been found to strongly differ in intrinsic water-use efficiency, defined as the ratio of CO_2 assimilation to leaf conductance to water vapour (A/g_s) and to seasonal soil drought sensitivity [7, 9, 27, 28, 29, 30, 34]. Several characteristics have been proposed to explain these differences, among which, differences in CO_2 assimilation rates [1, 6, 7, 29], stomatal regulation [7, 9, 23, 26, 29] or hydraulic conductivity [9, 39, 41]. Differences in water acquisition strategies among species and the ability of some species to explore deep soil layers could also explain these differences. For instance, Huc et al. [29] suggested that differences in stomatal sensitivity to seasonal soil drought between pioneer and late stage canopy tree species might be related to differential soil water extraction depth, late stage species being able to explore deeper soil layers. Alexandre [1] observed that a strong and deep taproot in some canopy tree species allowed them to extract water

in deeper layers and to avoid seasonal drought stress. It is generally thought that the rooting system of most trees in the wet tropics is concentrated in the upper soil layer [20, 35]. However, Canadell et al. [10] reviewed several studies on the maximum depth of trees in the wet tropics and found an average maximum depth of 6.5 ± 2.5 m, with a maximum as deep as 18.0 m [35]. It has also been found that the depth of the rooting system of some tropical tree species might partly depend on the type of soil drainage [20]. These results emphasise the need for more thorough investigations of the differences in rooting depth among tropical canopy tree species growing in different soil drainage type conditions and their consequences on leaf gas exchange.

We used the $\delta^{18}\text{O}$ methodology in a natural tropical rainforest of French Guiana and compared the depth of water extraction of two species, *Dicorynia guianensis* Amshoff and *Eperua falcata* Aublet, two Caesalpiniaceae growing together on different soil drainage types. It is hypothesised that (1) *E. falcata* may develop a deep rooting system which allows avoidance of seasonal soil drought stress [5, 7, 29, 30], (2) in contrast, *D. guianensis* cannot avoid seasonal soil drought because of its shallow rooting system [24, Atger, personal communication], (3) soil drainage types influence the depth of water extraction by the trees.

2. MATERIALS AND METHODS

2.1. Study sites

This study was performed in a natural forest near Petit-Saut dam, French Guiana ($5^\circ 20' \text{ N}$, $52^\circ 10' \text{ W}$, altitude 30 m). This forest was chosen because several dominant canopy trees of the two studied species were found next to each other on two sites differing in soil drainage and distant only by hundred meters. Two to three trees per studied species and per site were selected for this study. One site (DVD: deep vertical drainage) is located on the top of a small hill and presents a reddish-brown sandy-loamy to sandy horizon down to at least 4.0 m, with a micro-aggregated structure. The other site (SLD: superficial lateral drainage) is located downhill and consists of a clayey-silty alterite with a compact appearance at the base (less than 1 m) which induces lateral drainage. The climate in French Guiana is characterised by a long dry season from mid-August to the end of November and a short dry-season in February-March. The remaining months experience heavy rains with maximum rainfall in April and May. Mean annual rainfall is 2900 mm at Petit-Saut and the daily mean temperature of 25.8° C is almost constant over the year. Measurements

and sampling in this study were conducted in the middle of the 1997 dry season (end October), more than two months after the last rain event, and in the middle of the 1998 wet season (end of May).

2.2. Soil water content and $\delta^{18}\text{O}$ of soil and xylem water

In both seasons, four holes per site in the vicinity of the studied trees were dug using a Dutch auger. Soil samples were collected every 0.1 m down to 0.3 m depth and then every 0.3 m down to 3.0 m depth. About 0.2 l of soil sample was immediately placed in hermetically closed glass containers and frozen once in the laboratory at $-25.0\text{ }^\circ\text{C}$ until water extraction. Separate soil samples at each depth were collected in tin canisters and sealed with plastic film for subsequent determination of gravimetric soil water content (SWC). SWC was determined by comparing fresh and dry weights (48 h at $110.0\text{ }^\circ\text{C}$) of soil from each depth. In both seasons, two external wood samples from each tree (opposite sides of the tree) were collected at breast height with a hatchet around midday. The outer bark was removed and the sapwood (0.05–0.10 l) was immediately placed in hermetically closed glass containers and frozen once in the laboratory at $-25.0\text{ }^\circ\text{C}$ until water extraction.

Water was extracted from soil and sapwood samples during a 12 h cryogenic vacuum distillation, and sealed in hermetically closed vials which were sent for stable oxygen isotope composition analysis ($\delta^{18}\text{O}$) (Centre de recherches géodynamiques, Thonon les Bains, France). $\delta^{18}\text{O}$ was calculated as:

$$\delta^{18}\text{O} (\text{‰}) = \frac{R_{\text{sample}} - R_{\text{smow}}}{R_{\text{smow}}} 1000, \quad (1)$$

where R_{sample} and R_{smow} are the $^{18}\text{O}/^{16}\text{O}$ ratio in the water sample and in the conventional standard (SMOW), respectively.

2.3. Rooting system description

The vertical extension of the rooting system of two large trees (dbh > 0.2 m) per species and per site, growing in the vicinity of the sampled trees was analysed. Large wells at the base of these trees were dug using manual tools down to a depth where the diameter of the taproot of the considered tree was lower than 5 mm. No other roots of the considered tree were observed at that depth which is considered as the lower end of root prospection hereafter. Superficial horizontal roots were also followed and described.

2.4. Leaf water potential and carbon isotope composition

For each tree and in both seasons, about twenty mature and sunlit leaves were sampled using the shotgun method. The midday leaf water potential (Ψ_{wm}) of three leaves per tree was measured using a pressure bomb (PMS Instruments Model 1000, Corvallis, Oregon, USA) [38]. Measurements were conducted between 11.00 and 13.30 on clear days. The remaining leaves were used for leaf carbon isotope composition ($\delta^{13}\text{C}$, ‰) measurements, which was calculated as:

$$\delta^{13}\text{C} (\text{‰}) = \frac{R_{\text{leaf}} - R_{\text{PDB}}}{R_{\text{PDB}}} 1000, \quad (2)$$

where R_{leaf} and R_{PDB} are the $^{13}\text{C}/^{12}\text{C}$ ratio in the sample and in the conventional Pee Dee Belemnite standard, respectively. Leaves were oven dried at $70\text{ }^\circ\text{C}$ for 48 h and were finely ground. A sub-sample of 1 mg of powdered material was combusted and analysed for ^{13}C composition using an isotope ratio mass spectrometer (Delta S, Finnigan MAT, Bremen, Germany) at INRA Nancy (France). Since the carbon isotope composition of atmospheric CO_2 was identical for the different species growing in common conditions, leaf $\delta^{13}\text{C}$ is negatively related to the time-integrated ratio of intercellular to ambient CO_2 concentration and positively related to the time-integrated leaf intrinsic water-use efficiency (A/g_s) [18].

3. RESULTS

The two species clearly differed in the vertical distribution of the rooting systems. *E. falcata* developed a strong tap-root which can prospect deep horizons, down to -3.5 m in the deep vertical drainage (DVD) site and -2.0 m in the superficial lateral drainage (SLD) site. Long horizontal roots (up to 15.0 m) were found in the upper horizons. Further down, only small (< 1.0 m long) lateral roots were observed. In *D. guianensis*, the rooting system densely colonised the upper horizon, with long and abundant lateral roots (up to 17 m), while depths of root prospection were lower than in *E. falcata* (down to 1.6 m and 1.0 m in the DVD and SLD sites, respectively).

Leaf $\delta^{13}\text{C}$ values were not significantly different between species in SLD, but were slightly less negative in DVD for *D. guianensis* than for *E. falcata* (table I). Midday leaf water potential (Ψ_{wm}) was similar in both seasons for *E. falcata*, but was slightly less negative in the dry season as compared to the wet season in *D. guianensis* (table I). For the two species, there was no significant effect of drainage type on leaf $\delta^{13}\text{C}$ or Ψ_{wm} values (table I).

Table I. Midday leaf water potential (Ψ_{wm}) in wet and dry seasons and leaf carbon isotope composition ($\delta^{13}C$) in dry season of two canopy tree species growing in a tropical rainforest of French Guiana on two different sites. The two sites differed in soil drainage type (DVD, deep vertical drainage; SLD, superficial lateral drainage). Values are means \pm 1 SE. Within one column, means with different letters are significantly different ($p = 0.05$; ANOVA followed by Tukey's comparison test).

Species	Season	Drainage type	Midday leaf water potential Ψ_{wm} (MPa)	Leaf carbon isotope composition $\delta^{13}C$ (‰)
<i>Dicorynia guianensis</i>	Dry	DVD	-1.6 ± 0.1^a	-27.0 ± 0.1^a
		SLD	-1.7 ± 0.1^a	-27.5 ± 0.2^{ab}
	Wet	DVD	-2.1 ± 0.1^b	-
		SLD	-1.9 ± 0.1^b	-
<i>Eperua falcata</i>	Dry	DVD	-1.9 ± 0.1^b	-28.9 ± 0.2^c
		SLD	-2.1 ± 0.0^b	-28.1 ± 0.2^{bc}
	Wet	DVD	-2.1 ± 0.1^b	-
		SLD	-1.9 ± 0.1^b	-

Soil water content (SWC) underwent pronounced seasonal changes down to 3.0 m depth in both sites. The difference in SWC between the wet and the dry season was higher in SLD than in DVD in the upper 0.4 m soil layer, whereas the reverse was observed between 0.4 and 0.8 m depth (figure 1). Below 0.8 m this difference was similar in both sites.

Vertical soil water profiles of $\delta^{18}O$ were distinct between the sites and the seasons (figure 2). In the dry season, surface enrichment ($\delta^{18}O$ values $> -3.0\text{‰}$) was noted in both DVD and SLD profiles. The greatest enrichment occurred in the DVD profile where maximum values approached -1.0‰ . In the wet season, a similar enrichment was observed in surface down to -0.6 and -0.4 m in DVD and SLD, respectively. In the deeper layers, soil water $\delta^{18}O$ gradually increased with depth in both seasons in DVD, but showed a rather complex sinusoidal pattern with depth in SLD. The daily $\delta^{18}O$ values of rainwater ranged from -4.4 to -1.5‰ (weighted average $-3.4 \pm 0.3\text{‰}$).

For each site and each season, $\delta^{18}O$ variability of xylem water within species was relatively low (figure 2). In DVD, xylem $\delta^{18}O$ values of both species corresponded to two main mean depth intervals of the soil water $\delta^{18}O$ profiles (dry season: around -0.2 and -3.1 m for *E. falcata* and around -0.3 and -2.8 m for *D. guianensis*; wet season: around -0.2 m and between -1.8 and -3.1 m for *E. falcata* and around -0.2 m and between -2.6 and -3.1 m for *D. guianensis*) (figure 2). In SLD, the xylem $\delta^{18}O$ values corresponded to two mean depth intervals for *E. falcata* (around -0.8 m and -1.8 m) in the dry season and one (around -0.4 m) in the wet season. For *D. guianensis*, they corresponded to three main areas (dry season: around -0.4 , between -1.0 and -1.6 m and between -2.4 and -3.2 m; wet season: around -0.2 and -0.7 m and between -2.6 and -3.2 m).

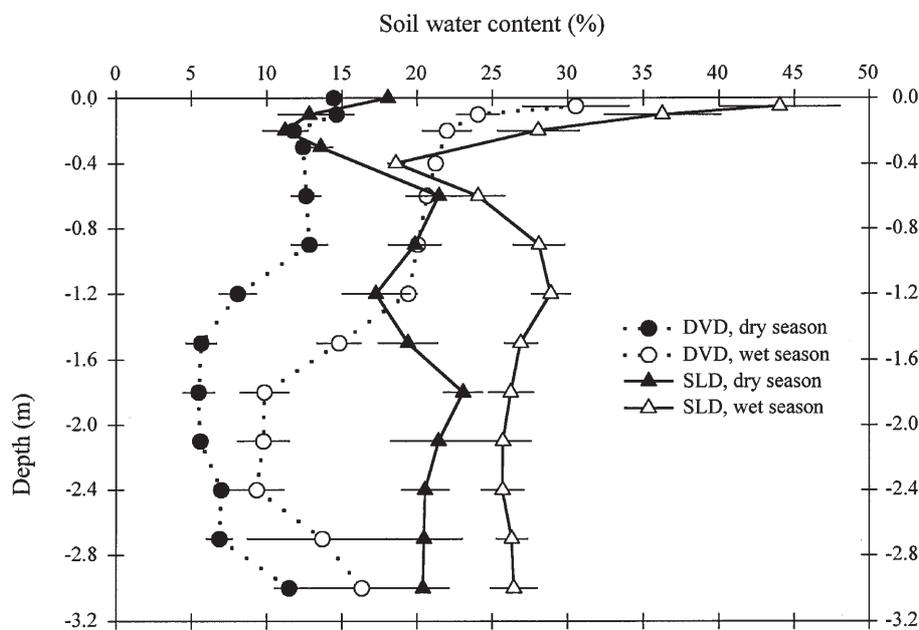


Figure 1. Vertical profiles of mean soil water content (± 1 SE, $n = 4$) on two sites differing in soil drainage type (DVD, deep vertical drainage; SLD, superficial lateral drainage) in the wet and the dry season.

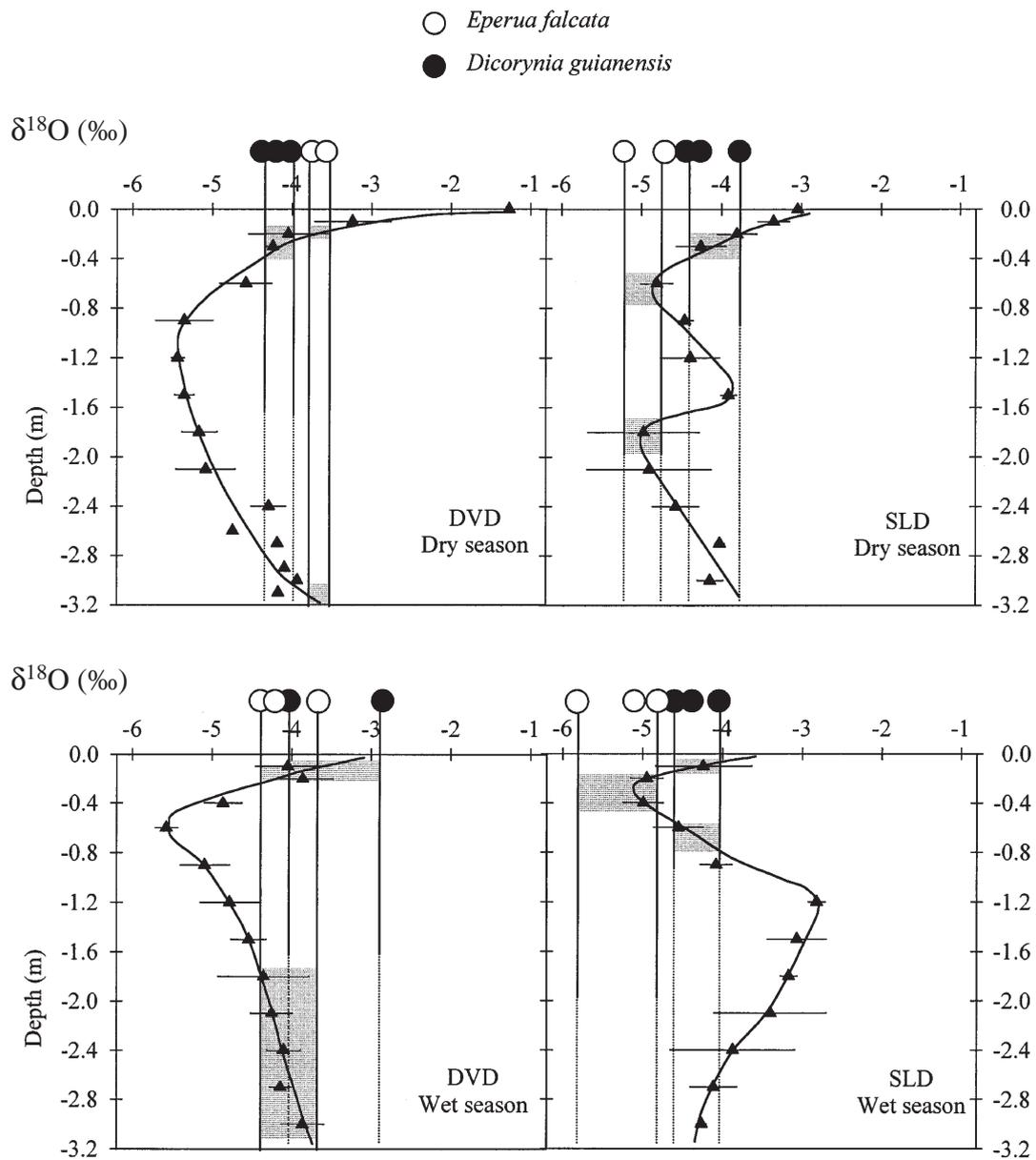


Figure 2. Xylem water oxygen isotope composition ($\delta^{18}\text{O}$) and vertical profiles of soil water $\delta^{18}\text{O}$ in a natural rainforest of French Guiana on two sites differing in soil drainage conditions (DVD, deep vertical; SLD, superficial lateral drainage) in the dry and the wet season. Xylem water samples were collected on two or three trees per species at each site. Soil water $\delta^{18}\text{O}$ values are mean values (± 1 SE) of four holes per site and per season. Dashed areas correspond to the estimated mean depth of soil water extraction for each species, site and season, based on water $\delta^{18}\text{O}$ estimations and rooting system observations. The projected xylem $\delta^{18}\text{O}$ values are represented in plain lines for root colonised horizons and in dotted lines for uncolonised horizons.

4. DISCUSSION

The description of the rooting system of the two species confirmed that the two species strongly differed

in rooting depth. On the site with deep vertical drainage (DVD), *E. falcata* can be considered as a deep-rooted species, with a tap-root which reaches more than -3.5 m. In contrast, *D. guianensis* mainly colonises the upper

1.0 m and seldom reaches more than -1.6 m. In restricted drainage (SLD), the compact layer near 1.0 m affected both species. *D. guianensis* roots were not able to penetrate this layer, whereas *E. falcata* roots crossed this layer but did not reach more than ca. -2.0 m. In contrast with published studies [22, 31, 43], differences in rooting depth between species were not related to marked differences in leaf $\delta^{13}\text{C}$ values – and thus in estimated intrinsic water-use efficiency – or in leaf water potential values (table 1). For both species, soil moisture conditions and soil drainage types had almost no effect on Ψ_{wm} , which suggests either that trees had access to sufficient water in the soil, or were able to regulate their leaf gas exchange, particularly stomata, in order to maintain high Ψ_{wm} values or even to increase it slightly in the dry season (*D. guianensis?*).

For each site and season, the variability of $\delta^{18}\text{O}$ of soil water at a considered depth was low. Similar results were noted by Bariac et al. [3] in a nearby natural rainforest. The profile of $\delta^{18}\text{O}$ of soil water with depth confirmed that daily atmospheric vapour pressure deficit, though relatively low in the natural rainforest [3, 21], can induce significant evaporation and ^{18}O enrichment in the upper soil layers (figure 2). This resulted in strongly decreasing $\delta^{18}\text{O}$ with depth in the upper 0.6 m in SLD and in the upper 1.0 m in DVD during the dry season. These results were similar to those observed by Jackson et al. [31]. The enrichment in ^{18}O of soil water further down in DVD, and the sinuous shape in SLD, could not be clearly interpreted. Bariac et al. [3] observed a similar enrichment from -0.3 to -1.0 m in the wet season in a natural rainforest of French Guiana. The combination of seasonal variations in the intensity of evaporation, highly variable $\delta^{18}\text{O}$ of rainwater, and water transfers in the soil via lateral drainage and water infiltration, might have contributed to the within profile variability.

The simple comparison of the ^{18}O signatures of xylem water and soil water did not allow us to provide any clear conclusions regarding the depth at which trees were extracting water. However, the combination of these results with the rooting system observations and the soil water content profiles brought about interesting results on the water acquisition strategies of these species growing in different drainage conditions.

In the dry season, in DVD, the $\delta^{18}\text{O}$ values of soil water and xylem water suggested that *E. falcata* roots could extract water both from the upper horizon and a horizon around -3.0 m depth (figure 2). Access to such deep horizons (more than -3.0 m) might be essential only during periods of severe water shortages in the upper horizon, as discussed by Tyree et al. [40]. Furthermore, such rooting characteristics might allow this species to access to other vital resources, such as

nitrate [Domenach, pers. comm.]. Soil drainage type had a strong influence on the depth of water extraction by *E. falcata*. In contrast to DVD, the isotopic signature of xylem water in SLD equalled that of soil water at the -0.6 or at the -1.8 m depth. Considering the sinuous shape of the soil water $\delta^{18}\text{O}$ profile, such an isotopic signature might well arise from the integration of soil water isotopic signatures of horizons between -0.6 and -2.0 m depth. These horizons indeed supported high fluctuations of water availability from the wet to the dry season (figure 1). Despite the strong differences in soil water availability from wet to dry season in both sites, the water status of *E. falcata* was affected neither by soil drought, nor by drainage type (table 1).

For both soil drainage types, *D. guianensis* developed a superficial rooting system and appeared to be able to extract water mainly in the upper 0.8 m (figure 2). The strategy of water acquisition of *D. guianensis* (i.e. shallow-rooted) might present some disadvantages as compared to species such as *E. falcata* (i.e. deeply rooted) [22, 43]. Potentially, there can be much greater competition for water and nutrient resources in the upper soil horizons. However, shallow-rooted species as *D. guianensis* might develop adaptive mechanisms such as partial [28, 29, 30, 34] or total [7] stomatal closure to tolerate or avoid soil drought, as confirmed by the lack of effect of either soil drainage type or seasonal soil moisture deficit on Ψ_{wm} in *D. guianensis*. It must be recalled here that *D. guianensis* has a high water-use efficiency as compared to other canopy tree species in French Guiana [9]. It has been suggested that water-use efficient species tolerate soil drought better than less efficient species [7, 8, 9]. Whether other shallow-rooted tree species would not suffer from these conditions is an important question. Differences in spatial distribution of species that were found to be related to soil structure and soil drainage type tend to confirm this hypothesis [1, 4, 5, 32, 37].

In conclusion, these results show that the methodology based on the natural abundance of ^{18}O of xylem and soil water has relatively low efficiency in this wet tropical system without data on root morphology and soil characteristics. This study suggests that combined studies of oxygen and hydrogen isotope labelled water supplied at different depth in the soil in the vicinity of studied trees might be promising to distinguish water acquisition strategies among wet tropical tree species [33]. Even though the two studied species presented highly different rooting habits, they both did not seem to suffer from the different soil drainage types and seasonal variations in water availability encountered in this forest. This could be associated to their high water-use efficiency. Whether this can be extended to other water-use

efficient species, or to less efficient species (low $\delta^{13}\text{C}$ values) is a worthy question.

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