Rainfall exclusion in an eastern Amazonian forest alters soil water movement and depth of water uptake[1]

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Deuterium-labeled water was used to study the effect of the Tapajós Throughfall Exclusion Experiment (TTEE) on soil moisture movement and on depth of water uptake by trees of *Coussarea racemosa*, *Sclerolobium chrysophyllum*, and *Eschweilera pedicellata*. The TTEE simulates an extended dry season in an eastern Amazonian rainforest, a plausible scenario if the El Niño phenomenon changes with climate change. The TTEE excludes 60% of the wet season throughfall from a 1-ha plot (treatment), while the control 1-ha plot receives precipitation year-round. Mean percolation rate of the label peak in the control plot was greater than in the treatment plot during the wet season (0.75 vs. 0.07 m/mo). The rate was similar for both plots during the dry season (ca. 0.15 m/mo), indicative that both plots have similar topsoil structure. Interestingly, the label peak in the control plot during the dry season migrated upward an average distance of 64 cm. We show that water probably moved upward through soil pores—i.e., it did not involve roots (hydraulic lift)—most likely because of a favorable gradient of total (matric + gravitational) potential coupled with sufficient unsaturated hydraulic conductivity. Water probably also moved upward in the treatment plot, but was not detectable; the label in this plot did not percolate below 1 m or beyond the depth of plant water uptake. During the dry season, trees in the rainfall exclusion plot, regardless of species, consistently absorbed water significantly deeper, but never below 1.5–2 m, than trees in the control plot, and therefore may represent expected root function of this understory/subcanopy tree community during extended dry periods.

Key words: *Coussarea racemosa*; deuterium; drought; eastern Amazonia; El Niño; *Eschweilera pedicellata*; global climate change; *Sclerolobium chrysophyllum*.

Numerous physiological studies have described the different strategies an individual plant uses to maintain homeostasis under dry conditions. These strategies involve intricately synchronized physiological mechanisms that include changes in stomatal conductance, photosynthesis rate, sap flow, water/osmotic potential, stem hydraulic conductivity (i.e., xylem vulnerability to cavitation), stem capacitance (water storage), vegetative/reproductive phenology, biomass accumulation (growth), biomass allocation (above- and belowground), leaf/stem tissue properties (e.g., elasticity), and chemical signaling/regulation (e.g., accumulation of proline, abscisic acid, dehydrins, ubiquitins, aquaporins) (see e.g., Taiz and Zeiger, 2002). While these mechanisms are relatively well understood in some species, the number of studies focusing on the response of whole communities to dry soil conditions is limited, because the feasibility of such studies depends on seasonal rainfall regimes or unpredictable droughts (e.g., Mulkey and Wright, 1996; Wright, 1996; Cao, 2000; Yavitt and Wright,

2001; Borchert et al., 2002; Engelbrecht et al., 2002; Potts, 2003). Experimental manipulations at the ecosystem level to study the effects of prolonged drought are even scarcer (e.g., Engelbrecht and Kursar, 2003), in part because the logistic effort required is immense but mainly because a significant reason must exist to justify such an experiment. Global climate change is one of them.

An extended soil drought in eastern Amazonia may be caused by El Niño episodes if global climatic conditions change in the future (Nepstad et al., 2002). In 1997–1998, for example, the strongest El Niño phenomenon of the past century was estimated, by a modeling approach, to have depleted soil water content in the soil to a depth of at least 5 m in an area of 1.5 million km² (Nepstad et al., 1999), a quarter of the whole Amazon basin. The drought dried the soil so intensively that surface fires—which in 50% of the cases occur by accident—extended over an area of at least 20 000 km², severely damaging pastures and mature Amazonian forests (Nepstad et al., 1999). The ecological response of the forest to these dry periods is not yet fully understood.

The Tapajós Throughfall Exclusion Experiment (TTEE), designed to simulate an extended drought period, is a large-scale manipulation working toward understanding the effect of dry conditions in the Amazon. The TTEE consists of two 1-ha plots in evergreen tropical seasonal forest in eastern Brazil, in which the understory of one of the plots (treatment plot) is covered with plastic panels (installed at 1–2 m height) throughout the wet season (Nepstad et al., 2002). This experiment is elucidating ecological, physiological and geochemical patterns at the community/ecosystem level that could occur under persistent dry conditions (e.g., patterns in vegetative and

reproductive phenology, leaf water potential, stem growth and respiration, litterfall, leaf-area index and canopy openness, photosynthesis, litter decomposition, biogeochemistry, and soil moisture dynamics, among others; Nepstad et al., 2002). The TTEE builds upon a pilot throughfall exclusion experience in the area of Paragominas, state of Pará, Brazil, which lasted from 1993 to 1996 (Cattânio et al., 2002).

In the eastern Amazon, as elsewhere, soil water depletion begins in the topsoil when evapotranspiration surpasses precipitation. In rainforests, the depletion is seasonal and the remaining water stored in deep soil layers is enough to support trees throughout the dry season (e.g., Nepstad et al., 1994; Jackson et al., 1995; Hodnett et al., 1996; Jipp et al., 1998; Meinzer et al., 1999). In fact, several studies have shown that many tropical tree species, including seedlings/saplings, physiologically adapt very well to seasonal dry conditions and that there is no significant mortality (e.g., Cao, 2000; Williamson et al., 2000; Engelbrecht et al., 2002; Engelbrecht and Kursar, 2003; Potts, 2003). The main objective of the TTEE, however, is to simulate a scenario of soil drought that elicits dramatic physiological responses. The ultimate cause of such expected water stress is the steady reduction of soil moisture, a phenomenon that should initially affect patterns of water uptake.

The uptake of water by different plant species or functional groups and the movement of pore water in the soil can be effectively studied using isotope technology. The techniques to study soil water movement in the unsaturated zone with isotope tracers were developed in the 1960s when water, in well structured soils, was demonstrated to diffuse or disperse little vertically or horizontally, and to infiltrate the soil by layers (Zimmermann et al., 1966, 1967a, b; Blume et al., 1967; Kline and Jordan, 1968). Concurrently with these studies, a technique to distinguish potential sources of soil water for plants using tritium or deuterium concentrations in the soil/plant continuum was also developed (Gonfiantini et al., 1965; Woods and O'Neal, 1965; Wershaw et al., 1970). However, the usefulness of this technique was not recognized fully until the late 1980s and early 1990s (White et al., 1985; Sternberg and Swart, 1987; Dawson and Ehleringer, 1991; Flanagan and Ehleringer, 1991; Walker and Richardson, 1991).

In Neotropical ecosystems, stable isotopes have proven useful to understand different natural processes. For example, tritium-enriched water was used near Manaus, Brazil, to study soil water balance (Araguás-Araguás et al., 1995), and natural abundances of deuterium were used in Central America and the Brazilian cerrado to study spatial and temporal partitioning of soil water by plants, probably as a result of competition (Jackson et al., 1995, 1999; Meinzer et al., 1999, 2001). These studies have been complemented by experiments using deuterium-enriched water (Moreira et al., 2000; Sternberg et al., 2002), which in fact have become increasingly common, particularly in temperate and subtropical zones (e.g., Bishop and Dambrine, 1995; Plamboeck et al., 1999; Turner et al., 2001; Schwinning et al., 2002; Peñuelas and Filella, 2003). The addition of an isotope label is particularly useful when the natural deuterium profile in the soil is convoluted and repetitive (i.e., with the same deuterium signature at different depths), thereby making a clear interpretation of plant water sources difficult (Moreira et al., 2000; Meinzer et al., 2001).

In this study, we investigated how the throughfall (i.e., rainfall) exclusion treatment affected (1) the percolation rate of soil moisture movement and (2) the depth of water uptake by understory to midcanopy trees. Exclusion of water inevitably
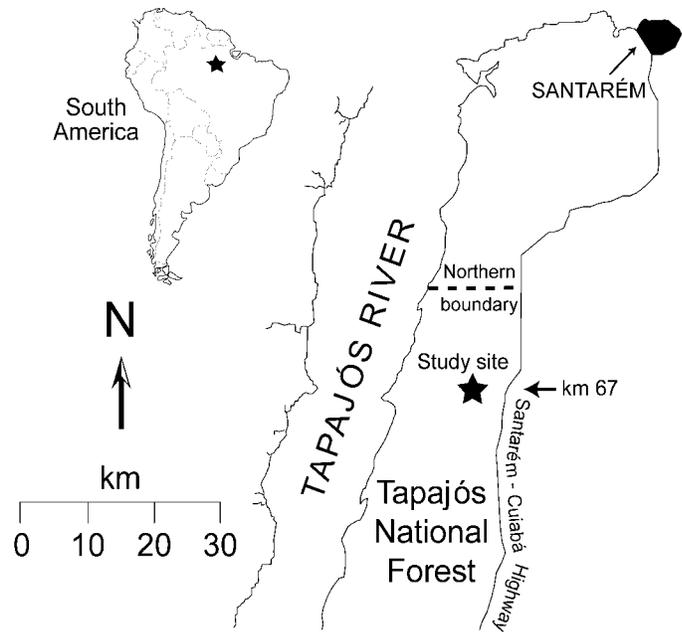

Fig. 1. Location of the Tapajós Throughfall Exclusion Experiment (black star) in Brazil (2°53′48.48″ S, 54°57′6.84″ W; Nepstad et al., 2002). Map modified from Parrotta et al. (1995) with permission.

diminishes percolation rate, but the intensity of this reduction in percolation was unknown. We knew nevertheless that the top 200 cm of soil of the treatment plot contained at least 100–150 mm less water than that of the control plot, and that deep water reserves in the treatment plot were apparently not being replenished (Nepstad et al., 2002; D. Nepstad et al., The Woods Hole Research Center, unpublished data). These factors led us to postulate that the depth of water uptake by trees shifted deeper in the treatment than in the control plots, especially in the dry season, but also in the wet season, when the panels are installed in the treatment plot simulating a dry season. The percolation rate of water and the depth of water uptake was investigated by irrigating a defined area of soil around various trees in the treatment and control plots with deuterium-enriched water at the start and end of the 2002 wet season. The deuterium label was followed in the soil profile and in wood cores/stems during the wet and dry seasons of the same year. The depth of water uptake was inferred using a conceptual model which estimates a mean depth of water uptake at a given time, based on the distribution of deuterium in the soil and the deuterium concentration in a plant.

MATERIALS AND METHODS

Study site—The TTEE is located in Tapajós National Forest, state of Pará, Brazil (2°53′48.5″ S, 54°57′6.8″ W, 150–200 m altitude; Nepstad et al., 2002; Williams et al., 2002; Fig. 1). The study area is flat terrain of old-growth upland forest, accessible by the Santarém-Cuiabá road. According to historical meteorological records from the nearby city of Santarém (1914–1981; www.worldclimate.com), mean annual rainfall is 2061 mm. Nepstad et al. (2002) reports an average rainfall of 2000 mm/yr, with a minimum of 600 mm and a maximum of 3000 mm, while Parrotta et al. (1995) reports an average rainfall of 1920 mm/yr. Dry season occurs from June/July to December, but is more pronounced (<100 mm monthly rainfall) from August to November (www.worldclimate.com). The mean monthly temperature is around 25–26°C (Parrotta et al., 1995; www.worldclimate.com).

The TTEE consists of two 1-ha plots with similar structure, diversity, floristics, biomass, topography, and soil characteristics (Nepstad et al., 2002). The plots are 25 m apart at their closest point (Nepstad et al., 2002). The soil in the area is an Oxisol (Haplustox) with 60% (Nepstad et al., 2002) to 90% clay content (Williams et al., 2002). The water table is 100 m deep (Nepstad et al., 2002). The treatment plot is covered with plastic panels, installed 1–2 m above the ground, during the wet season. This prevents 50% of the rainfall (60% of the throughfall) from reaching the soil (Nepstad et al., 2002). The other plot serves as the control and is never covered with plastic panels. The first throughfall exclusion period started in early February 2000, after a 1-yr calibration period (1999) in which both plots were closely monitored to define pretreatment conditions (Nepstad et al., 2002). To avoid lateral infiltration of soil water, a trench 1 m wide × 1.7 m deep was excavated around each of the plots and lined with plastic (Nepstad et al., 2002). In the treatment plot, the water collected by the plastic panels evacuates into the trench, and then into a deeper drainage ditch that ends in a small valley (Nepstad et al., 2002). The trenches prevent water infiltration from the outside to a depth of at least 2–3 m (Nepstad et al., 2002; L. Sternberg, University of Miami, personal observation).

Irrigation design and study species—The first irrigation experiment started on 7 January 2002, and the second on 16 May 2002. These months correspond to the start and end of the wet season, respectively. We selected three species of understory to midcanopy trees shared by both plots: *Coussarea racemosa* A. Rich. ("caferana," Rubiaceae), *Sclerolobium chrysophyllum* Poepp. ("taxi vermelho," Leguminosae-Caesalpinioideae), and *Eschweilera pedicellata* (Rich.) S. A. Mori ("mata-matá liso," Lecythidaceae). The ecophysiology (e.g., sap flow, photosynthesis rate) of these and other focal species in the plots is being monitored by the TTEE scientific team. *Coussarea racemosa*, typically an understory tree of height ≤10 m, is the most common tree species in both plots; *S. chrysophyllum*, usually 15–20 m tall, is the third most common shared species; and *E. pedicellata*, generally 10–15 m tall, is the seventh most common shared species (D. Nepstad et al., The Woods Hole Research Center, unpublished data on vegetation structure from the plots).

In each of the two experiments, five trees of each species were irrigated in each plot (Appendix 1, see Supplemental Data accompanying online version of this article). The same individual trees in the treatment plot were used for both the first (7 January 2002) and second irrigation (16 May 2002) experiments because we predicted that the label in the treatment plot would remain close to the surface and any further irrigation with deuterium-labeled water would only reinforce it. We randomly selected adult trees having a diameter at breast height (DBH) ≥10 cm, but, in order to sample the same number of individuals of each species, we occasionally had to select individuals <10 cm DBH when there were no adult trees available (Appendix 1, see Supplemental Data accompanying online version of this article). If a tree in the treatment plot grew within 5 m of a very large tree (DBH > 1 m), it was not selected because stemflow from the large tree could overwhelm the throughfall exclusion treatment.

In each irrigation experiment, 8 L of a solution made of 99% D_2O (Icon Services, Summit, New Jersey, USA) and local water was evenly sprinkled around the trunk of each tree on a circular area with a radius of 1.5 m, where most of the water-absorbing roots of adult small trees are apparently found (Sanford and Cuevas, 1996; Sternberg et al., 2002). The δD of the solution irrigated was around 130 000‰. The litter around each tree was removed before the irrigation to ensure percolation of the deuterium label into the soil profile. The litter was replaced immediately after irrigation. No extra water was added to push the label into the soil because this would have affected the throughfall exclusion treatment. The 8 L of deuterium-labeled water represents 1 mm of rain. In the control plot, this amount of water is equivalent to 23% of the average daily throughfall (0.06% of the average annual throughfall), while for the treatment plot it represents 32% of the average daily throughfall (0.08% of the average annual throughfall).

Sample collection—The label of the first irrigation (7 January 2002, day 0) and the second irrigation (16 May 2002, day 0) experiments was traced by collecting soil and plant samples at periodic time intervals during the wet and dry seasons of 2002.

Soil samples—Samples for the first irrigation experiment were collected in both plots on day 2, day 8, and day 17. In the control plot, soil samples were also taken on day 128, day 156, and day 281. Samples for the second irrigation experiment were taken on day 6, day 27, and day 152. Background deuterium levels were assessed in soil cores sampled to a depth of at least 80 cm in a nearby area, outside the plots, on 8 January 2002 ($N = 3$ cores) and 24 January 2002 ($N = 1$). At each sampling date, the soil from two to six irrigated areas around the trees, randomly selected, was sampled using a manual soil auger (Forestry Suppliers, Inc., Jackson, Massachusetts, USA). A soil core (one per irrigated area) consisted of soil samples (approximately 7–26 g of wet soil) taken at the surface and at various sampling depths. Sampling depths were intended to include the whole deuterium pulse in the soil (i.e., samples were taken down to a depth below the expected depth of the deuterium peak at the time of collection). We collected the soil samples in clear 25 × 150 mm screw-cap culture glass tubes and sealed them immediately around the cap with Parafilm M (Thomas Scientific, Inc., Swedesboro, New Jersey, USA) to avoid any isotope fractionation due to evaporation.

Plant samples—Wood cores (approximately 5 cm long and 5 mm diameter) at breast height (130 cm) were collected from *C. racemosa* and *S. chrysophyllum* trees using a Haglöf Increment Borer (Forestry Suppliers, Inc., Jackson, Massachusetts, USA). Wood cores from *E. pedicellata* could not be collected because of its very dense hardwood; instead, we collected stems (approximately 8 cm long × 8 mm diameter) with a complete covering of cork (complete periderm) to avoid fractionation due to evaporation. Samples for the first irrigation experiment were collected on day 8 and day 17 in both plots. In the control plot, samples were also taken on day 130, day 156, and day 281. Samples for the second irrigation experiment were collected on day 6, day 27, and day 152 in both plots. Background deuterium levels were measured in plant stems from a nearby area outside the plots on 9 January 2002 ($N = 7$ stems), 12 January 2002 ($N = 3$), 24 January 2002 ($N = 10$) and 22 May 2002 ($N = 6$). Wood cores and stems were collected in vacutainers (13 × 100 mm; Becton Dickinson, Franklin Lakes, New Jersey, USA) that were immediately sealed with the vacutainer's rubber cap and Parafilm. Because the samples were transported via airplane, air in the vacutainers was evacuated with a syringe to reduce pressure.

Water extraction and deuterium measurements—Soil and plant samples were shipped to the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (University of Miami, Miami, Florida, USA) or to the Centro de Energia Nuclear na Agricultura (Universidade de São Paulo, Piracicaba, São Paulo, Brazil). Once they arrived, the samples were stored in a freezer at −10°C.

Procedures for water extraction and measurement of deuterium concentration followed standard procedures (see e.g., Moreira et al., 2000; Sternberg et al., 2002). Samples were first thawed overnight to ambient temperature (20°C) and then placed in a cryogenic vacuum distillation system. Water collected in this manner was stored in small scintillation vials with waterproof caps (Fisher Scientific Co., Suwanee, Georgia, USA). The hydrogen from the water was extracted using a modified version of the Coleman et al. (1982) method: (1) Three μL of water were mixed in an ampule with 150 mg of Zn reagent (Biogeochemical Laboratories, Indiana University, Bloomington, Indiana, USA) previously outgassed at 350°C for 10 min, (2) the ampule was frozen in liquid nitrogen and sealed under high vacuum, and (3) hydrogen gas was produced by placing the ampule in an oven for 2 h at 500°C. The deuterium content of the hydrogen gas sample was measured with a Micromass Prism II dual-inlet isotope ratio mass spectrometer (Micromass Inc., Waters Corporation, Milford, Massachusetts, USA) and/or a Finnigan Mat Delta E mass spectrometer (Thermo Electron Co., Bremen, Germany). The average precision of the spectrometers was ±0.14 δD units.

Deuterium content is expressed as δD values, which represent the relative difference per mil (‰) between the deuterium isotopic composition of a sample and that of Vienna Standard Mean Ocean Water (VSMOW; Craig, 1961).

The isotopic composition is calculated using the atomic ratio (R) of "heavy" isotopes to "light" isotopes. In this case, R is the atomic ratio of deuterium hydrogen (^2H or simply D) to protium hydrogen (^1H or simply H):

$$\delta D = \left[\frac{(D/H)_{\text{sample}}}{(D/H)_{\text{SMOW}}} - 1 \right] \times 1000 \qquad (1)$$

Data analysis—Data from the first irrigation experiment covered the period from January, the start of the wet season, to October, mid-dry season. Data from the second irrigation experiment covered the period from May, near the end of the wet season, to October, mid-dry season. To simplify the interpretation, all data from the second irrigation experiment were considered dry season data.

Soil samples—Soil δD values at each sampling date were averaged and plotted against depth to show the migration of the label in the soil. We developed a MATLAB (The MathWorks Inc., Natick, Massachusetts, USA) program to calculate the expected δD values for every cm in the soil profile via a cubic spline interpolation using the observed mean δD values. We used this program to calculate the mean depth of peak deuterium concentration in the soil for each sampling date. The spline interpolation was represented in the figures by a curve, which was graphed using SigmaPlot (Systat Software Inc., Point Richmond, California, USA). Data from 9 January 2002 sampling (day 2 after the first irrigation) was not graphed because the soil cores on that day were taken only 20 cm deep. Soil water in the irrigated areas at any depth was considered enriched when it was above the highest background value ($\delta D = -12$‰).

In addition, to understand how the amount of rain reaching the soil affects the vertical movement of water in the soil, we did a correlation analysis between the depths of peak deuterium concentration and the amount of throughfall accumulated over time, in the presence and in the absence of panels. The treatment plot was assumed to have no panels installed on 22 May and 12 June 2002, even though the panels in reality started to be removed on 1 July 2002. This approach is justified because there was no significant difference between the amount of throughfall under the panels in the treatment plot and the amount of throughfall in the control plot from 22 May to 1 July 2002 (two-tailed t test: $t = 1.56$, $P = 0.12$, $N = 40$ d).

Plant samples—We used a one-tailed t test to evaluate if δD values of plant samples were significantly higher than background deuterium levels at each sampling date. Because no independent plant sampling of background deuterium levels was done for the 12 June and 15 October 2002 sampling dates, data from these dates were compared to the 22 May 2002 background data.

Model to determine mean depth of water uptake by plants—To estimate the mean depth of water uptake by a tree at a given time, the δD values in the soil profile and the δD value of sap water were coupled in a model. Sap water data used in the model met the following criteria: (1) deuterium concentration of water sampled at a given date was significantly greater than background levels (at least in one of the plots), (2) sufficient time had already passed for the label to migrate to the sample point (breast height in case of wood cores, or lowest accessible branch in case of stems), so that equilibration of the deuterium concentration in the soil–plant continuum had probably been attained, and (3) data for a given date was available for both plots. Data from the following sampling dates complied with the three criteria: 24 January 2002 (day 17 after first irrigation), 12 June 2002 (day 27 after second irrigation), and 15 October 2002 (day 152 after second irrigation). Data from day 8 of the first irrigation experiment and day 6 of the second irrigation experiment did not meet the second criterion, and therefore were not used in this analysis. Furthermore, the time water (i.e., the deuterium label) takes to migrate to the sample point varies between treatment and control trees during the throughfall exclusion months (wet season) because average sap flow velocity of the treatment trees is usually 50% slower than that of the control trees, taking at least 3–5 d for water to migrate from upper soil layers to the sample point (D. Nepstad et al., The Woods Hole Research Center, unpublished data).

The model, written in MATLAB (Appendix 2, see Data Supplement ac-

companying the online version of this article), was constructed with two assumptions and one axiom.

Assumption 1—We assumed that, at any given time, a tree can take up water from a 50-cm vertical segment of soil at any depth in the soil profile. The following reasoning was used to support this assumption. During 3 yr of time-domain-reflectometry (TDR) measurements of volumetric water content in the soil (January 2000–November 2002), the maximum daily average at depths of 0.3, 0.5, 1, 2 and 3 m, for both plots, was 0.35 cm³/cm³, while the minimum average was 0.25 (Nepstad et al., 2002; D. Nepstad et al., The Woods Hole Research Center, unpublished data). Thus, assuming that the difference between the maximum TDR and the minimum TDR is due solely to evapotranspiration, each cm of soil provides an average maximum of 1 mm of water for evapotranspiration ($0.35 - 0.25 = 0.1$; i.e., 1 mm per cm of soil). Because daily evapotranspiration in these forests is on the average around 4 mm/d (Leopoldo et al., 1995; Hodnett et al., 1996; Jipp et al., 1998; Costa and Foley, 1999), plants must acquire water every day from a vertical segment of soil approximately 4 cm long.

There may be differences in the length of soil segment used by different species of trees to harvest water, especially between dry and wet seasons. In a typical dry season, the mean number of consecutive days without rainfall (according to 2000, 2001 and 2002 rainfall measurements; D. Nepstad et al., The Woods Hole Research Center, unpublished data) is 7 d. To sustain the transpiration demand during those 7 d when no precipitation falls and the soil is not recharged with rain, plants must be able to extract water from at least 28 cm of soil ($=4$ cm soil/d $\times$ 7 d). Furthermore, the maximum number of continuous days with no rain from January 2000 to December 2002 was 25. During these extended dry periods, plants must be able to extract water from at least 100 cm of soil ($=4$ cm soil/d $\times$ 25 d) to sustain transpiration. The length of the vertical soil segment (50 cm) used in this study falls within the range of these two estimates and is a conservative approximation. Any error in our assumption regarding the length of soil segment used by plants will lead to only slight changes in the conclusions because the model output is not very sensitive to this parameter. The mean depths of water uptake calculated with a 50-cm segment were linearly correlated with those calculated with a 20-cm segment ($r = 0.898$, slope $= 0.91$, $P < 0.001$) and with those calculated with a 80-cm segment ($r = 0.877$, slope $= 0.90$, $P < 0.001$). The slopes of the correlations suggest that for a 60% change in the parameter (i.e., length of soil segment), there is only a 10% change in model output (i.e., calculated mean depths of water uptake).

Assumption 2—We assumed that the amount of water taken up by a tree is not the same at all depths throughout the 50-cm segment, but instead is taken up according to a normal distribution (Sokal and Rohlf, 1995):

$$n_i = \frac{1}{\sigma\sqrt{2\pi}} e^{-(Y-\mu)^2/2\sigma^2} \qquad (2)$$

where n_i is the proportion of water taken up at a depth Y, and μ is the mean depth of water uptake. The proportions (n_i) always add up to one, except when the normal curve approaches the surface or the lower depth limit and is truncated. In those cases, the proportions were corrected by weighing them against the area under the curve so they always sum to one. A normal distribution of the depth of water uptake means that 99.7% of the water comes from a 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, the standard deviation (σ) of this normal distribution is equal to 8.33 cm. We also assumed that trees do not acquire water from two distinct regions of the soil profile because this phenomenon has been demonstrated only in arid regions where there are two distinct water sources available for plant uptake, either the water table or rain water (e.g., Dawson and Ehleringer, 1991; Schwinning et al., 2002).

Axiom 1—The axiom is supported by mass balance principles and states that the deuterium signature in the plant stem/trunk water can be interpreted as the sum of the deuterium signatures of the soil water absorbed at different depths (Moreira et al., 2000). In the model, therefore, the deuterium signature

in the plant sample is equal to the sum of the deuterium signatures at all the 1-cm interval depths within a given 50-cm segment, weighed by the proportion of water uptake at each cm as described by the normal distribution (Eq. 1). This can be expressed as (Moreira et al., 2000):

$$\delta D_c^{plant} = \sum_{i=1}^{m} (n_i \times \delta D_i^{soil}) \tag{3}$$

where δD_c^{plant} is the calculated hydrogen isotopic composition of plant trunk/stem water, m is the maximum depth analyzed, and δD_i^{soil} is the average isotopic composition of soil water at the ith depth. For every position of the 50-cm segment of water uptake, as it moves deeper and deeper in the soil profile by 1-cm increments until depth m, there is a calculated mean depth of water uptake (μ). Therefore, for a given deuterium profile in the soil, there are m possible δD_c^{plant} values, each with a corresponding mean depth of water uptake (μ). Those mean depths at which δD_c^{plant} is equal to the observed δD value of the actual sample measured in the lab (δD_o^{plant}) are considered solutions.

In some cases, assuming a soil segment of water uptake of 50 cm, no solution was possible, i.e., δD_o^{plant} did not match any δD_c^{plant} at any depth. We excluded these trees from the data analysis. The effect of their exclusion is probably minimal because they represent only 11% of the total number of samples analyzed ($N = 90$ samples). On the other hand, in eight of the 90 samples analyzed, two or three solutions for the mean depth of water uptake were found. Even though plants are likely taking water from only one of these depths, we averaged these mean depths and treated them as a single observation for data analysis. The mean depths of water uptake (μ) of the trees in each species were averaged and compared between the two plots using an independent two-tailed t test.

RESULTS

Soil water movement—First irrigation experiment: wet and dry seasons 2002—During the wet season of 2002 (January–May), the deuterium-labeled water percolated at a mean rate of 0.75 m/mo in the control plot, and 0.07 m/mo in the treatment plot (Fig. 2). On 15 May (128 d after the first irrigation), the deuterium peak in the control plot had reached an average depth of 254 cm while in the treatment plot the peak had only reached an average depth of 29 cm (Fig. 2). During the dry season (which starts around June), the deuterium-labeled water in the control plot not only stopped percolating but actually moved back upward (Table 1, Figs. 2 and 3): by 15 October ($N = 2$ soil cores) the deuterium peak rose to an average depth of 190 cm, i.e., 64 cm shallower than the 15 May mean depth ($N = 4$ soil cores), a difference that is statistically significant ($P = 0.046$, one-tailed t test). In the treatment plot, we were not able to observe upward movement of the deuterium label at 2 m depth because the deuterium did not percolate deeply (Fig. 2).

Two days after the irrigation, on 9 January, the peak deuterium concentration in the treatment plot (mean $\delta D \pm 1$ SE $= 10\,348 \pm 2568$; $N = 7$ soil cores) was significantly greater ($P = 0.03$, two-tailed t test) than that in the control plot (mean $\delta D \pm 1$ SE $= 3427 \pm 696$; $N = 6$). As the deuterium percolated down the soil profile, the concentration in both plots kept decreasing. However, by 15 May, the difference in the peak deuterium concentrations between the plots had become much less obvious than that of 15 January (Fig. 2).

Second irrigation experiment: dry season 2002—During the dry season of 2002, the deuterium label in both plots percolated downwards at a similar mean rate (approximately 0.15 m/mo; Fig. 4). Thus, by 15 October (152 days after the May irrigation) the label peak had percolated to similar depths in both plots (30 cm in the control, and 41 cm in the treatment; Fig. 4, Table 1). The depths of these peaks were similar to the depth reached by the peak in the treatment plot during the wet season (29 cm; Fig. 2), while the panels were in place simulating a dry season. Upward movement of the second label during the dry season in deeper soil layers was not observed in either plot because the deuterium did not percolate deeply (Fig. 4). As in the first irrigation, the deuterium concentration in both plots decreased over time (Fig. 4).

Effect of precipitation on the percolation of deuterium—Downward movement of the deuterium peak was linearly correlated with throughfall, regardless of whether or not the panels were present (both $P \leq 0.01$; Fig. 5). Under natural (no panels) conditions (i.e., during the dry season in the treatment plot and all year long in the control plot), every cm of rain "pushed" the soil water a distance of about 2 cm (1 : 2 relationship; slope $= 1.88$, $r = 0.98$, $P < 0.0001$; Fig. 5). On the other hand, depths of deuterium peaks in the treatment plot when the panels were in place were approximately half the amount of accumulated throughfall (slope $= 0.45$, $r = 0.99$, $P = 0.01$; Fig. 5). The correlation under natural conditions was strengthened by the inclusion of four data points (represented as triangles in Fig. 5) obtained from another deuterium irrigation experiment conducted in the same site, next to the TTEE plots, from March 1999 to January 2000 (Sternberg et al., 2002). The three extreme points (upper right corner of Fig. 5) do not represent variation of the data, but only an artifact of sampling frequency. The statistical significance of the linear correlation does not depend on these extreme points because if they are excluded from the analysis the correlation is still significant and the approximate 1 : 2 relationship is maintained (slope $= 2.28$, $r = 0.928$, $P < 0.001$).

Patterns of plant enrichment and mean depths of water uptake—After 17 d of the first irrigation, average δD values of sap water from all tree species in both plots were significantly above background (Table 1). A similar result was found 27 d after the second irrigation (Table 1). This initial deuterium enrichment decreased over time, but not at a constant rate across species or individuals. For example, *E. pedicellata* was still significantly enriched 130 d after the first irrigation in the control plot, and three *C. racemosa* control trees (9–164, 9–189, 9–201; Appendix 1, see Supplemental Data accompanying online version of this article) became significantly enriched again in October after being at background levels at least since 17 May ($P \ll 0.001$, Z test using -41.2, the mean background δD value of 12 June, as the population mean). Although the enrichment of these three trees increased the mean δD of all five *C. racemosa* trees to -15.2, this mean was not significantly higher than background levels (Table 1).

The mean depths of water uptake, as calculated by the model, follow similar patterns across the three species studied. Further, the differences in the mean depth of water uptake between control and treatment plots, at a given date, were significant or almost significant for all three species (two-tailed t test; Fig. 6). On 24 January, 17 d after the first irrigation, at the onset of the wet season, trees in the control plot were on average taking up water at 63 cm deeper than the trees in the treatment plot, which at that time was covered by the panels (Fig. 6). This pattern reversed on 12 June (the start of the dry season, 27 d after the second irrigation) and 15 October (mid-dry season, 152 d after the second irrigation), when the treatment
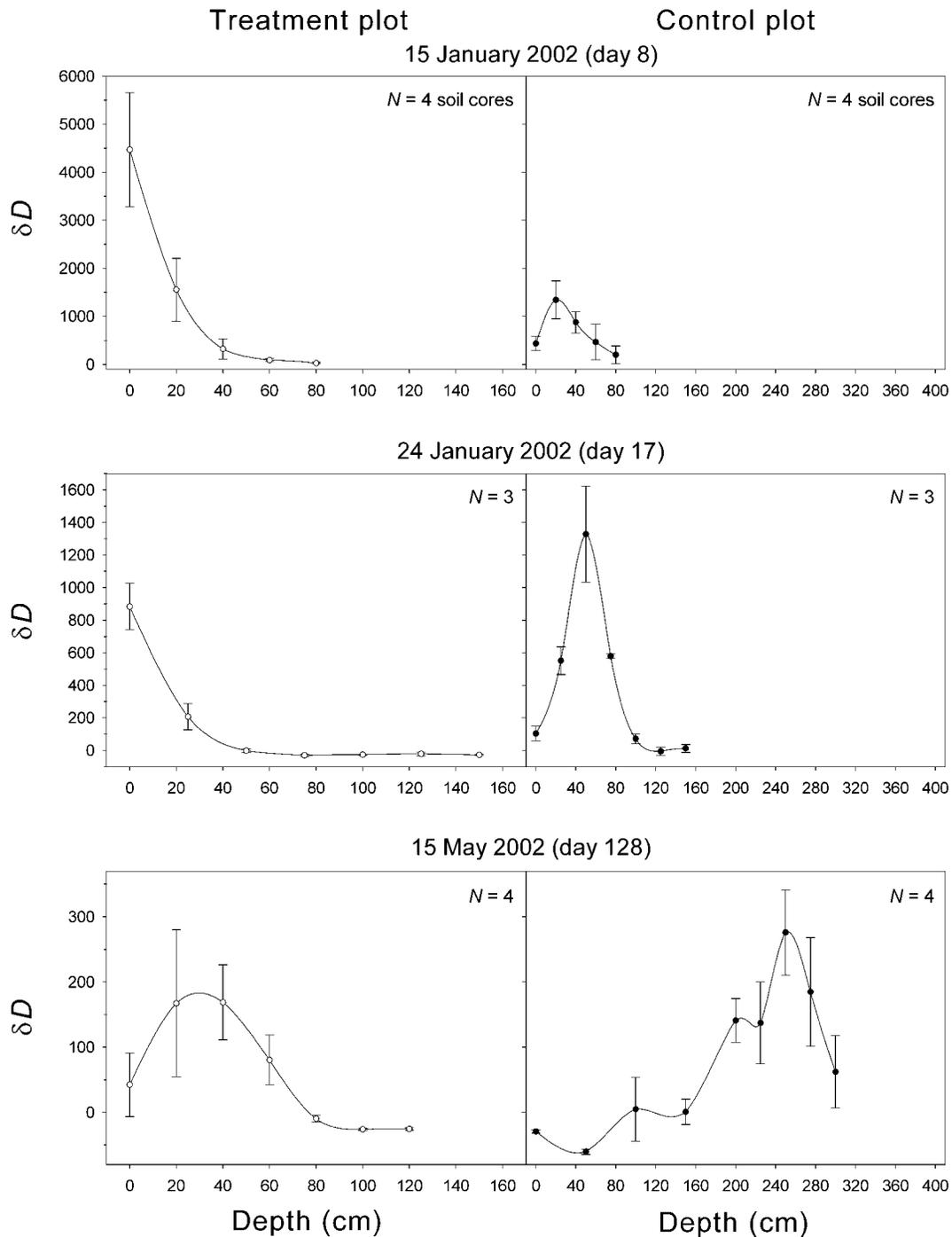
Fig. 2. Movement of deuterium-labeled water in the soil profile (depth) in the first irrigation experiment at the Tapajós Throughfall Exclusion Experiment, in Brazil. Trees were irrigated at the start of the wet season on 7 January 2002. In 2002, the treatment plot was covered with panels from 1 January to 1 July. Note the scale differences of the δD axis as the deuterium concentration in the soil diminishes over time. δD units represent the per mil (‰) relative difference between the deuterium isotopic composition of a sample and that of an international standard (V-SMOW, with $\delta D = 0$). Error bars represent ± 1 SE.

trees were taking up water at greater depths than the control trees (Fig. 6). On average, on 12 June and 15 October, treatment trees harvested water at a depth 26 cm and 37 cm deeper than control trees, respectively (Fig. 6). As the dry season progressed from June to October, trees in both plots tended to take up water at greater depths (Fig. 6).

DISCUSSION

Rain regulates the percolation of water in the soil profile, but water may also move upward—During the 2002 wet season, the percolation rate in the control plot (0.75 m/mo) was an order of magnitude higher than that in the treatment plot

TABLE 1. Deuterium isotopic composition (mean $\delta D \pm 1$ SD) of the plant samples from the trees irrigated with deuterium-labeled water ($N = 5$ trees per species in each irrigation experiment) at the Tapajós Throughfall Exclusion Experiment, in Brazil. Asterisks (* = $P \leq 0.05$, ** = $P \leq 0.01$) denote significantly higher δD values (one-tailed t test) with respect to background control δD values of non-irrigated trees. The trees in the treatment plot were used for both irrigations, while a second set of trees in the control plot was selected for the second irrigation (see Materials and Methods, *Irrigation design and study species*; Appendix 1). The depth range at which the soil was enriched with deuterium (i.e., soil δD at that depth range was above the maximum background soil δD value measured: −12‰), and the mean depth of peak deuterium concentrations are also shown (see Materials and Methods, *Data analysis* for further explanation).

Date	Control plot					Treatment plot				
	Coussarea racemosa (cores)	Sclerolobium chrysophyllum (cores)	Eschweilera pedicellata (stems)	D-enriched depth range (cm)	Mean depth of peak (cm)	Coussarea racemosa (cores)	Sclerolobium chrysophyllum (cores)	Eschweilera pedicellata (stems)	D-enriched depth range (cm)	Mean depth of peak (cm)
First irrigation experiment (7 January 2002)										
24 January (day 17)	207.8 ± 139.3**	39.6 ± 75**	−1.8 ± 31.6**	0–150	50	608.0 ± 216.5**	105.9 ± 95**	41.3 ± 68.6**	0–55	0
15/17 May (day 128/130)	−39.1 ± 5.9	−31.2 ± 10.9	−10.5 ± 6.3**	84–300	254					
12 June (day 156)	−41.2 ± 2.6	−33.9 ± 9.5	−21.2 ± 3.6	142–319	233					
15 October (day 281)	−15.2 ± 25.9	−37.3 ± 9.2	−20.8 ± 9.9	97–300	190					
Second irrigation experiment (16 May 2002)										
12 June (day 27)	150.0 ± 81.8**	−1.1 ± 23.9*	0.5 ± 17.6**	0–50	19	176.6 ± 80.5**	6.1 ± 36.3*	68.9 ± 56.3**	0–92	20
15 October (day 152)	−6.2 ± 18.9*	−35.8 ± 8.3	−22.2 ± 3.6	0–59	30	29 ± 22.2**	−16.3 ± 17.2	3.1 ± 15**	0–126	41

(0.07 m/mo; Fig. 2), therefore demonstrating that the panels had significantly reduced the percolation of water in the soil profile. The percolation rate in the treatment plot in the wet season (0.07 m/mo; Fig. 2), when the panels were in place, was even lower than the rate in the dry season (around 0.15 m/mo; Fig. 4). In a physically homogeneous soil profile, percolation is mainly regulated by amount and frequency of rainfall and initial soil moisture conditions. On 16 May 2002, the day of the second irrigation at the onset of the dry season, volumetric soil water content at a depth of 30 cm differed by an average of 0.13 cm³/cm³ between the control and treatment plots (0.39 vs. 0.26, respectively; D. Nepstad et al., The Woods Hole Research Center, unpublished data). This difference in volumetric soil water content, however, had little effect on the percolation rate because both plots showed similar rates (ca. 0.15 m/mo; Fig. 4). This confirms that physical characteristics of the topsoil are alike in both plots and that the main factor regulating the downward movement of water in the plots is rain input (Araguás-Araguás et al., 1995; Moreira et al., 2000; Sternberg et al., 2002). The rates reported in this study are within the range published in the literature for humid tropical forest soils (Kline and Jordan, 1968; Araguás-Araguás et al., 1995; Moreira et al., 2000; Sternberg et al., 2002), although the 2002 wet season percolation rate in the control plot may be the highest ever reported (0.75 m/mo).

The 1 : 2 relationship between cumulative throughfall and depth of deuterium peak under natural conditions (Fig. 5) can be explained by considering that saturated volumetric water content of this forest soil is ca. 0.5 cm³/cm³ (Nepstad et al., 2002; D. Nepstad et al., The Woods Hole Research Center, unpublished data). This means that around 50% of a volume unit of clay soil is water, while the other 50% is either solid matter or entrapped air, which explains why 1 cm of rain can only fit in a soil column if the water from 2 cm of soil is displaced. This 1 : 2 relationship between the amount of cumulative rainfall and the depth of the deuterium peak does not apply in the presence of panels (Fig. 5) probably because of rapid loss of water by plant uptake and/or evaporation at or near the soil surface.

Water in the soil profile at depths >2 m can move upward several decimeters during a dry season (Fig. 3). A similar, although less conspicuous, pattern was also found in a seasonal forest and abandoned pasture in the eastern Amazon (Moreira et al., 2000), confirming this phenomenon. From the end of the wet season (15 May) to the middle of the dry season (15 October), the deuterium peak on average moved up from 254 cm to 190 cm (Figs. 2 and 3, Table 1). This means, assuming that the 1 : 2 relationship described previously (Fig. 5) is applicable in this situation as well, that 32 cm of water moved up during this period, an amount comparable to the rainfall falling during the wettest months (March and April; climate data on Santarém in www.worldclimate.com).

Soil physics theory states that upward movement of water can be explained by an upward gradient of total potential (matric + gravitational) coupled with sufficiently high unsaturated hydraulic conductivity (see e.g., Marshall et al., 1996). Roots may create this gradient potential because of greater water absorption at or near the soil surface, which creates a lower potential than in the soil layers below. Complementarily, the gradient can also be caused by soil evaporation. If water is redistributed from deep to shallow soil layers through roots, the process is commonly known as "hydraulic lift" (Richards and Caldwell, 1987; Dawson, 1996). In this study, however, water
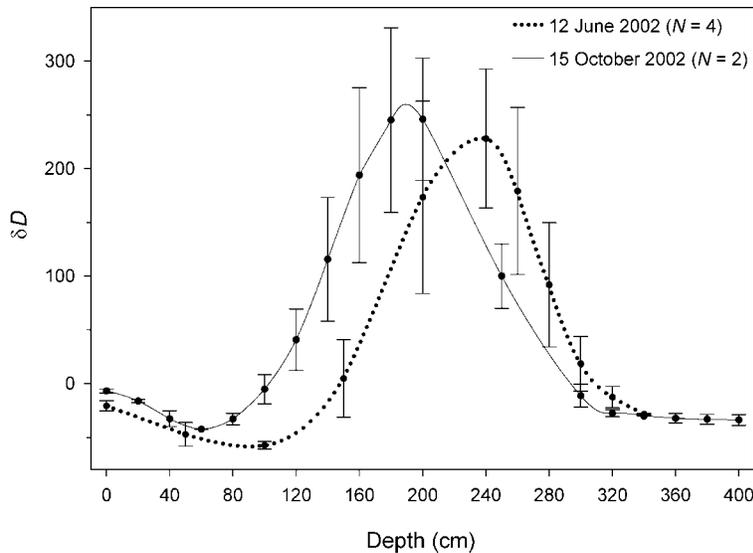
Fig. 3.   Upward movement of the deuterium-labeled water during the 2002 dry season in the control plot at the Tapajós Throughfall Exclusion Experiment, in Brazil. Irrigation took place on 7 January 2002 (first irrigation experiment). The dotted line represents the 12 June sampling (day 156; $N = 4$ soil cores) and the continuous line the 15 October sampling (day 281; $N = 2$). δD units represent the per mil (‰) relative difference between the deuterium isotopic composition of a sample and that of an international standard (V-SMOW, with $\delta D = 0$). Error bars represent ± 1 SE.

most probably was not transported through roots. If roots were absorbing water from moist (deep) soil layers and depositing it in drier (shallow) soil layers, the deuterium label in the soil should clearly reflect this process because in general there is no isotopic fractionation by plant roots (Gonfiantini et al., 1965; Wershaw et al., 1970). If roots harvested up water at 2.5 m depth and then deposited it around 2 m (or less) night after night, the 15 October deuterium profile should show a second peak around 2 m (Fig. 7). Alternatively, if hydraulic lift occurred gradually throughout the soil profile, as expected if the fine root distribution is continuous, then the deuterium profile curve should have an extended tail (Fig. 7). Neither of these possible deuterium profiles was observed in this study, and therefore we suggest that, in tropical forests, when little or no rain falls for a relatively long period of time, significant amounts of water can move upward from depth not through roots (hydraulic lift), but through soil pores. In fact, given that micropores (5–30 μm) and ultramicropores (0.1–5 μm) occur in clay soils, water in capillaries of this size could be driven upward several meters if a significant water potential gradient in the soil profile is present. The extent of this upward movement and its effect on the water relations of eastern Amazonian forests certainly merits further study.

Water uptake at depths >2 m is minimal—The rapid loss of deuterium from the surface of the soil is typical of irrigation studies with a hydrogen-isotope tracer (e.g., Araguás-Araguás et al., 1995; Moreira et al., 2000; Sternberg et al., 2002) and is probably related to evaporation, equilibration with ambient vapor, or dilution of the label in the water already present at the soil surface (Zimmermann et al., 1966, 1967a, b; Blume et al., 1967; Münnich, 1983). At depths >50 cm, evaporation is minimal and therefore loss of the label must be related to dilution caused by mixing of deuterium-labeled water with incoming precipitation and/or local soil water, coupled with plant water uptake (Woods and O'Neal, 1965; Zimmermann et al., 1966, 1967a, b; Blume et al., 1967; Münnich, 1983;

Araguás-Araguás et al., 1995; Moreira et al., 2000; Sternberg et al., 2002). However, no decrease in deuterium concentration was observed below 2 m depth (e.g., the δD value of the 15 May peak from the first irrigation in the control plot is very similar to the δD values of the 12 June and 15 October peaks; Figs. 2 and 3). This leads to the conclusion that plant water uptake at depths >2 m must be minimal (see also Sternberg et al., 2002), which, regarding the discussion in the previous section, is further evidence against the possibility that hydraulic lift was the cause of upward movement of water in the control plot from approximately 2.5 to 2 m depth during the 2002 dry season.

δD of sap water from all tree species in the control plot were significantly enriched as long as soil water close to the surface had δD values above background (Table 1). By 17 May, after downward percolation of the deuterium label caused the soil to be above background from 0.84 to 3.0 m deep, only one species (*E. pedicellata*) had sap water with δD values significantly above background levels (Table 1). None of the species was enriched after the label had percolated further downward, and the soil water was above background only at depths >1.42 m (by 12 June; Table 1). Therefore, the individuals studied here—some of which had a DBH as large as 20–26 cm (Appendix 1, see Supplemental Data accompanying online version of this article) and buttresses extending 0.5 m or more from the trunk (particularly *S. chrysophyllum*)—were not accessing soil water to a substantial degree much beyond 1 m. This is puzzling when considered in the context of the observed decrease in soil moisture in the control plot down to at least 3 m during the dry seasons (Nepstad et al., 2002), and the presence of fine roots at that depth, although at a much lower density than at the surface (D. Nepstad et al., The Woods Hole Research Center, unpublished data). A possible solution to this problem is the observation of the upward movement of the deuterium label during the dry season (Fig. 3). Plants may access a substantial amount of deep soil moisture through this route rather than by direct water uptake at
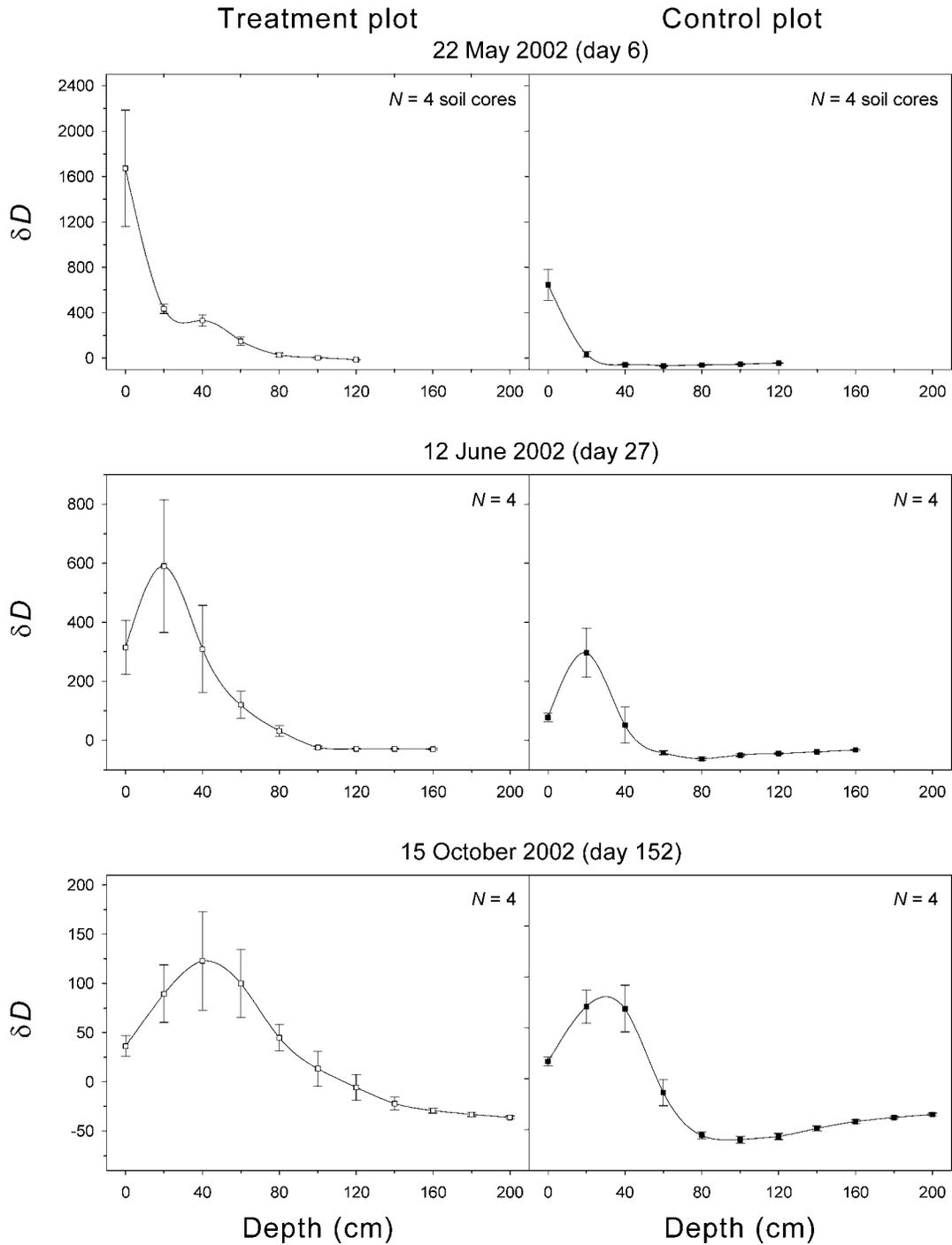
Fig. 4.   Movement of deuterium-labeled water in the soil profile (depth) in the second irrigation experiment at the Tapajós Throughfall Exclusion Experiment, in Brazil. Trees were irrigated at the end of the wet season on 16 May 2002. Panels in the treatment plot were removed on 1 July, at the onset of the dry season. Note the scale differences of the δD axis as the deuterium concentration in the soil diminishes over time. δD units represent the per mil (‰) relative difference between the deuterium isotopic composition of a sample and that of an international standard (V-SMOW, with $\delta D = 0$). Error bars represent ±1 SE.

depth. Evidence supporting this hypothesis can be seen in the changes of the δD values of sap water from *C. racemosa* control trees in the first irrigation experiment: by October 15, when the deuterium label had moved upward in the soil profile, three of the five individuals of *C. racemosa* became unexpectedly enriched in deuterium (Z test, $P \ll 0.001$; see Re-

sults). It is also possible that deep water is accessed only by larger trees (DBH ≥ 50 cm), but this pattern has not been supported by other studies in neotropical forests. For example, Meinzer et al. (1999), in Barro Colorado Island (Panamá), observed that, during the dry season, relatively small trees tend to get water from deeper layers of the soil profile compared
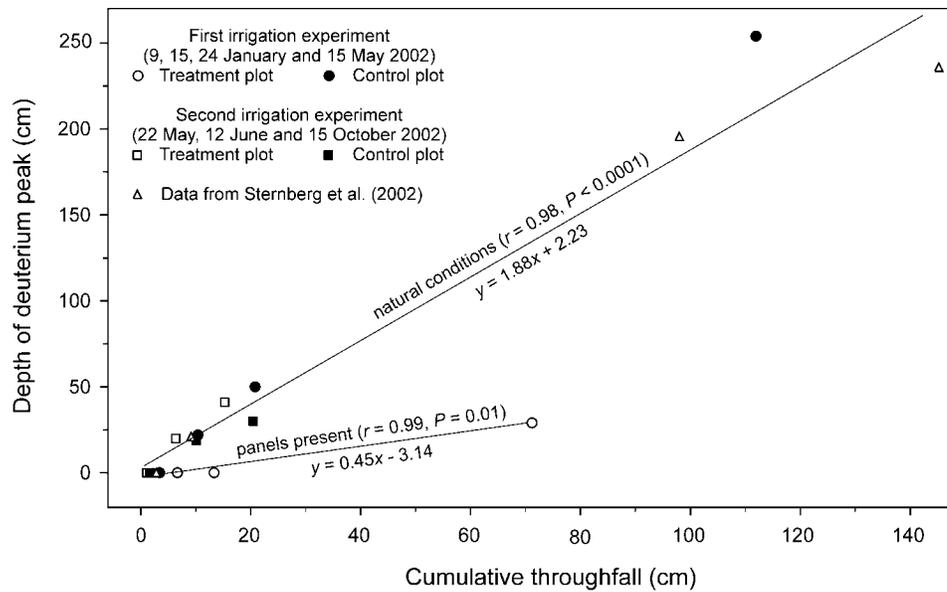
Fig. 5.   Relationship between depth of deuterium peak in the soil profile and cumulative throughfall reaching the soil under natural conditions (three data sources: treatment plot during the dry season [mostly without panels], control plot all year long, and forest site nearby the plots reported by Sternberg et al., 2002) and when it is covered by panels (one data source only: treatment plot during the wet season). The 12 June and 15 October 2002 samplings for the first irrigation experiment in the control plot were excluded from this analysis because the deuterium peak was moving upward. The 22 May and 12 June 2002 data for the second irrigation experiment in the treatment plot were analyzed as if the panels already had been removed, although they were actually removed on 1 July 2002 (see Materials and Methods, *Data analysis* for further explanation).
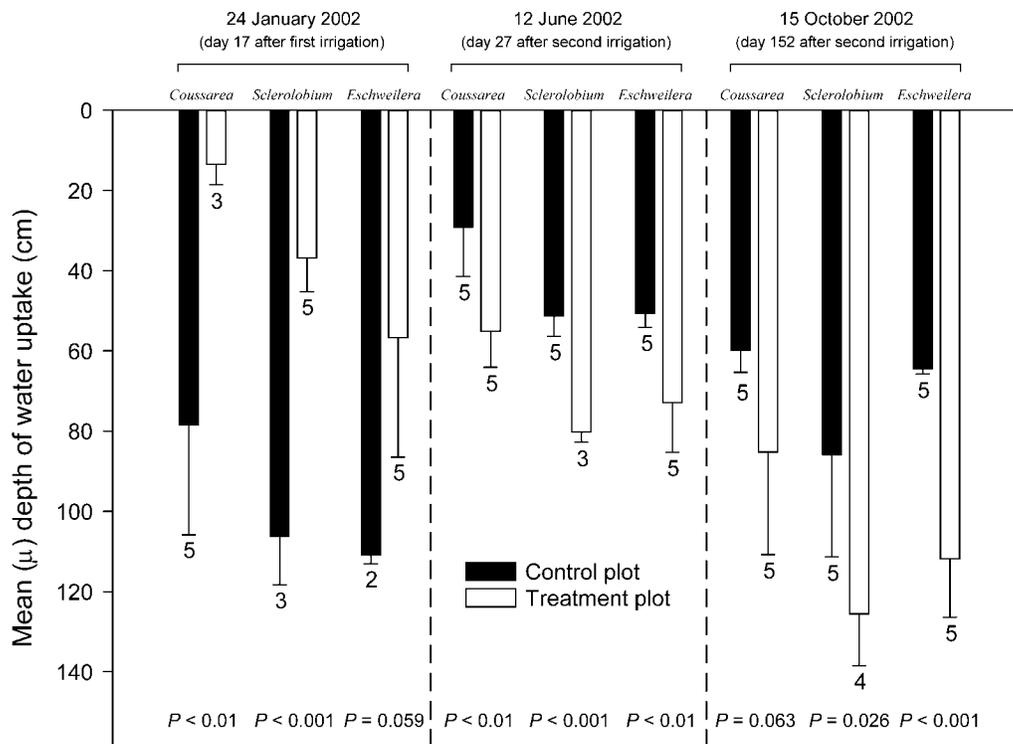

Fig. 6.   Mean depths of water uptake (μ) by *Coussarea racemosa*, *Sclerolobium chrysophyllum*, and *Eschweilera pedicellata* trees, as inferred from the deuterium signatures of the plants (see Table 1) and the deuterium profiles of the soil (see Figs. 2 and 4). The mean depths were calculated using a conceptual model (see Materials and Methods, *Data analysis*). The number below each column is the sample size (*N*), i.e., the number of trees (of five in each species) that had a solution in the model. The probabilities (*P*) of a two-tailed *t* test performed between control and treatment plots are also shown. Error bars represent ±1 SE.
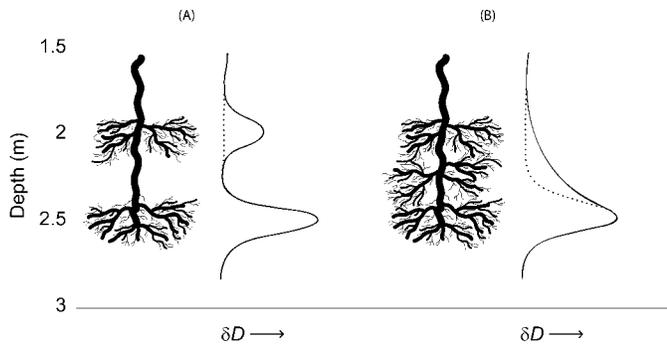
Fig. 7. Expected profiles of deuterium concentration in the soil as a consequence of hydraulic lift, and possible root distributions explaining such profiles. Full functionality of all roots shown is assumed. The y-axis represents the approximate depths at which upward movement of water was observed in this study (from 2.5 m to 2 m; Table 1, Figs. 2 and 3). The original deuterium profiles are indicated by a dotted line which overlaps the expected deuterium profile at certain depths. (A) Water is absorbed by the roots at 2.5 m and deposited in the soil at 2 m; as a result, two δD peaks should be observed. This is the classic model of hydraulic lift, except that plants may also deposit the absorbed water closer to the surface. (B) Water is absorbed by the roots at 2.5 m and gradually deposited in the soil profile above this depth; as a result, the δD value of the soil layers above 2.5 m should steadily increase over time.

to larger trees. In addition, Sternberg et al. (1998), in Fazenda Victória (eastern Brazil), showed that there is no vertical distinct segregation of roots in the soil horizon with respect to tree size.

***Treatment trees tap water at significantly greater depths than control trees, but also respond to seasonal stimuli*—** Because water content is much lower in the surface of the treatment plot and therefore is more quickly depleted (Nepstad et al., 2002), it was expected that treatment trees would access water from deeper layers of the soil profile. Indeed, mean depths of water uptake by treatment trees were deeper than those of control trees in June (end of 2002 wet season) and October (mid 2002 dry season) (Fig. 6). All three species had this pattern, with some species in the treatment plot accessing water as much as 0.5 m below that accessed in the control plot (Fig. 6). Superimposed on the difference in depth of water uptake between treatment and control plants is a seasonal effect: during the end of the wet season (June) both treatment and control trees were on average harvesting water from shallower layers of the soil profile (0.3–0.8 m) than during the mid-dry season (0.6–1.25 m; Fig. 6). The similarity in depth of water uptake response implies that fine roots apparently function and are distributed in a similar way among these three unrelated species of trees.

The January sampling (at the start of the 2002 wet season) did not conform to our expectations because, on average, trees in the treatment plot were actually accessing soil water from shallower, not deeper, layers of the soil profile than control trees (0.13–0.57 m vs. 0.79–1.11 m, respectively; Fig. 6). The simplest explanation of this phenomenon is that the irrigation with 8 L of deuterium-labeled water (1 mm of rain) around each tree in the treatment plot moistened the soil surface enough to induce fine root production and the subsequent absorption of moisture at that layer of the soil profile. The enriched water was sprinkled on a relatively litter-free soil (see Methods), which may have reinforced this effect. A comple-

mentary explanation is that substantial throughfall and stemflow leaked between the panels at the very beginning of January 2002 (e.g., 162 mm from 1 January to 24 January; D. Nepstad et al., The Woods Hole Research Center, unpublished data), which induced superficial fine root growth around the trunks from root primordia that were latent during the strong 2001 dry season. As a result, treatment trees may have quickly switched their strategy from deep to shallow water uptake at the start of the 2002 wet season, independent of the addition of the deuterium-labeled water (7 January). In fact, a major increase in fine root production at 50 cm depth in the treatment plot has been observed at the start of a wet season (D. Nepstad et al., The Woods Hole Research Center, unpublished data). Rapid superficial fine root production in response to rain has also been observed in other studies in the tropics (e.g., Sanford and Cuevas, 1996; Cao, 2000; Yavitt and Wright, 2001).

Shallow fine root production in response to the first wet season rains has also been observed in the control plot (D. Nepstad et al., The Woods Hole Research Center, unpublished data) but, at least at the very beginning of the 2002 wet season, the bulk of water uptake seemed to still occur at depths around 1 m (0.79–1.11 m, on average; Fig. 6). The water at these depths was probably enough to sustain transpiration demand because it had not been depleted by the throughfall exclusion treatment and was being quickly recharged by infiltrating precipitation (see de Souza et al., 1996; Nepstad et al., 2002). This could be the situation throughout the wet season, although we lack data to support this speculation. When the frequency and intensity of rains began to decrease in June (a transitional month between wet and dry seasons), the control as well as the treatment trees eventually conformed to the expected trend: control trees tapped water at shallower depths than treatment trees (Fig. 6) because of higher depletion of surface water content in the treatment plot than in the control plot (D. Nepstad et al., The Woods Hole Research Center, unpublished data).

***Conclusions*—**In 2002, we applied deuterium-enriched water around selected understory/subcanopy trees in the treatment and control plots of the Tapajós Throughfall Exclusion Experiment (see Nepstad et al., 2002) to describe differences between plots in regards to (1) seasonal movement of soil pore water in the soil profile, and (2) depth at which such moving water is taken up by the trees.

During the wet season, the percolation rate in the treatment plot was lower than that in the control plot because the plastic panels effectively simulated a dry season. During the dry season, when the panels were removed and/or both plots received the same rainfall, the percolation rates of treatment and control plots were very similar, indicating similar physical characteristics between both plots. Interestingly, upward water movement was detected with the deuterium label in the control plot during the dry season. This phenomenon was probably caused by an upward gradient of total potential (matric + gravitational) and sufficient unsaturated hydraulic conductivity in the soil. We argue that this water mostly moved through soil pores, not through roots (hydraulic lift), but further studies should confirm or reject this postulate. Upward water movement most likely occurred in the treatment plot as well, but was not detected because the label did not percolate deeply in this plot.

The three different tree species responded in a similar manner to the throughfall exclusion treatment in regards to the depth at which they harvested water and therefore may be

representative of other understory/subcanopy trees in the plots. In the dry season, treatment trees obtained most water at deeper soil layers than control trees (although never below 1.5–2 m). This was expected because the wet-season throughfall-exclusion treatment, which started in February 2000, significantly reduced water content of the top soil layers in the treatment plot (Nepstad et al., 2002), probably reducing fine root biomass and function.

How the depth of water uptake by different life forms will change as the water content of the soil in the treatment plot continues to diminish is unknown. The understory/subcanopy trees, especially during the dry season, may continue to harvest water even deeper, but is unknown if other life forms (e.g., lianas) or life stages (e.g., seedlings or large trees with DBH $\geq$ 50 cm) will respond in similar ways. This kind of ecophysiological information is important to understand how eastern Amazonian forests would respond in the event of extended droughts, which are expected during El Niño years because of global climate change (Nepstad et al., 2002).

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