UNIVERSITY OF MIAMI

EFFECT OF RAINFALL EXCLUSION ON SOIL MOISTURE MOVEMENT
AND DEPTH OF WATER UPTAKE BY AMAZONIAN TREES

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EFFECT OF RAINFALL EXCLUSION ON SOIL MOISTURE MOVEMENT 
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Dry periods caused by El Niño phenomena may last longer in eastern Amazonian forests as a result of global climate change. Among the various responses of the forest to these expected droughts, the functionality of roots and soil water movement are not yet well understood. I used the experimental setup of the Tapajós Throughfall Exclusion Experiment (TTEE) —a large-scale experiment in Pará, Brazil, that simulates an extended drought—to study the effect of rainfall (throughfall) exclusion on the seasonal movement of soil moisture and the seasonal changes in depth of water uptake by three locally abundant species of trees: *Coussarea racemosa* A.Rich., *Sclerolobium chrysophyllum* Poepp., and *Eschweilera pedicellata* (Rich.) S.A.Mori. The TTEE started in January 2000 and consists of two 1-ha plots: treatment and control. The soil of the treatment plot is covered by plastic panels during the wet season. Deuterium-enriched water was sprinkled in both plots around different individuals of each species on January 7, 2002 (first irrigation experiment, beginning of the wet season) and on May 16, 2002 (second irrigation experiment, end of the wet season). Soil and plant samples were collected on day two, day five, day eight, day 17, day 130, day 156 and day 281 after the first irrigation, and on day six, day 27 and day 152 after the second irrigation. The movement of water in unsaturated clay soils also was investigated using a simple model based on the Richards equation. The depth of water uptake was inferred using another model which estimates a mean depth of water uptake based on the distribution of deuterium in the soil and the level of deuterium enrichment observed in plant stem/trunk water.

During the wet season, when the treatment plot was covered with panels, the mean percolation rate of water in the control plot (0.75 m/month) was much higher than in the treatment plot (0.07 m/month). During the dry season, the water in both plots percolated at the same mean rate (0.15 m/month). In the control plot every centimeter of rain typically displaced the soil water a distance of about two centimeters. During the dry season, the peak of deuterium concentration in the soil of the control plot moved upwards, from ~2.5 m to ~2 m. I show that this upward movement of water can not be explained by hydraulic lift. However, it can be explained by capillary rise in clay soils, a postulate verified by the model of soil water movement. An analysis of the $\delta D$ values from plants and soil through time indicated that water uptake at depths >2 m was minimal. Treatment trees, independent of species, harvested water significantly deeper than control trees, particularly by the end of the wet season and throughout the dry season.
To Pauli,
for your profound understanding.
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INTRODUCTION

Numerous physiological studies, mostly experiments, have described the different strategies an individual plant or population uses to maintain homeostasis under dry conditions. These strategies involve intricately synchronized physiological mechanisms that include changes in stomatal conductance (leaf gas exchange), sap flow, water-use efficiency (and hence photosynthesis), 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 below-ground), 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 1991, Jones 1992, Dias-Filho and Dawson 1995, Milnes et al. 1998, Davies and Gowing 1999, Bacon et al. 2002, Koslowsky and Pallardy 2002, Siemens and Zwiazek 2003, Snyder and Williams 2003). While these mechanisms are well understood on an individual or species level, 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 natural events, such as seasonality or unpredictable drought periods (e.g. Wright 1992, Mulkey and Wright 1996, Oren et al. 1996, Wright 1996, Cao 2000, Yavitt and Wright 2001, Borchert et al. 2002, Engelbrecht et al. 2002, Brodribb et al. 2003, Potts 2003). Experimental manipulations at the community level to study the effects of prolonged drought are even more scarce, in part because the logistic effort required is immense but mainly because few significant reasons exist to justify such an experiment. Global climate change is one of them.

An extended soil drought 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 depleted soil water content in the soil to a depth of at least five meters in an area of 1.5 million km$^2$ (Nepstad et al. 1999), a quarter of the whole Amazon basin. The drought dried out 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 km$^2$, severely damaging pastures and mature Amazonian forests (Nepstad et al. 1999). The ecological response of the whole forest to these dry periods is not yet
fully understood, but the Tapajós Throughfall Exclusion Experiment (TTEE), designed to simulate an extended drought period, is a large-scale experimental manipulation working towards this objective. The TTEE consists of two 1-ha plots in an evergreen tropical seasonal forest in eastern Brazil. The soil of one of the plots (treatment plot) is covered with plastic panels throughout the wet season (Nepstad et al. 2002). This experiment will help to elucidate ecological, physiological and geochemical patterns at the community/ecosystem level that could occur under persistent drought 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. Usually, 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 several tropical tree species, including seedlings/saplings, adapt so well to seasonal dry conditions that overall physiological performance is almost unaffected and no significant mortality occurs (e.g. Condit et al. 1995, Cao 2000, Williamson et al. 2000, Gilbert et al. 2001, Engelbrecht et al. 2002, Potts 2003). The main objective of the TTEE, however, is to simulate a scenario of soil drought that elicits dramatic physiological responses in the vegetation. 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.

Strategies of soil water uptake by different plant species or functional groups is an area of current intensive research in tropical ecosystems, mostly concentrated on the spatial and temporal partitioning of soil water as a result of competition (Meinzer et al. 2001). This area of research (patterns of soil water uptake by plants coupled with 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 1960’s when it was demonstrated that, in general, water infiltrates the soil by layers which show limited vertical/horizontal diffusion or dispersion (Zimmermann et al. 1966, 1967a, 1967b, Blume et al. 1967, Kline and Jordan 1968). Concurrently with these studies, the 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 validity of this technique was not recognized fully until the late 1980’s and early 1990’s (White et al. 1985, Sternberg and Swart 1987, Dawson and Ehleringer 1991, Flanagan and Ehleringer 1991, Walker and Richardson 1991). Studies of plant water sources in tropical soils using natural abundances of stable isotopes are relatively recent (Jackson et al. 1995, 1999, Meinzer et al. 1999), and have been complemented by experiments with deuterium-enriched water (Moreira et al. 2000, Sternberg et al. 2002). In fact, plant physiological experiments with deuterium- or tritium-enriched water have become increasingly common in the last ten years, particularly in the temperate zone (e.g. Bishop and Dambrine 1995, Plamboeck et al. 1999, Turner et al. 2001, Schwinning et al. 2002, Peñuelas and Filella 2003).

The natural abundances of deuterium in the soil can provide information to determine potential sources of soil water used by plants (e.g. Sternberg and Swart 1987, Dawson and Ehleringer 1991). However, when the natural deuterium profile in the soil is convoluted and repetitive (i.e. showing the same deuterium signature at different depths), a clear interpretation may not be feasible. This is the case in many terra-firme Amazonian forests (see e.g. Moreira et al. 2000). To override such convoluted natural pattern and therefore clarify future data interpretation, one can add deuterium-enriched water to the soil (Moreira et al. 2000, Meinzer et al. 2001, Sternberg et al. 2002). This approach makes it possible to also study the movement of water in the soil (Zimmermann et al. 1966, 1967a, 1967b, Blume et al. 1967, Kline and Jordan 1968, Araguás-Araguás et al. 1995, Moreira et al. 2000, Sternberg et al. 2002).

In this study, I investigated the effect of the rainfall (throughfall) exclusion treatment on seasonal movement of soil moisture and on seasonal changes in the depth of water uptake by understory to mid-canopy trees. Given that at 50 cm depth, the soil in the treatment plot is increasingly drier than the control plot (Nepstad et al. 2002) —a
phenomenon that should inhibit fine root production in the topsoil (Sanford and Cuevas 1996)—I initially postulated that (1) the percolation rate of soil water in the treatment plot will be lower than in the control plot, particularly during the wet season when the panels are in place; and (2) the depth of water uptake by trees will shift deeper in the treatment than in the control plot, especially in the dry season, but also in the wet season. These postulates were investigated by irrigating a defined area of soil around different trees from each species in the treatment and control plots with deuterium-enriched water. The deuterium label was then followed in the soil profile and in plant stems/wood cores during the wet and dry seasons of 2002.

To help explain the results obtained with the deuterium label, the movement of water in clay soils was also investigated using a simple model based on the Richards equation (Richards 1931), i.e. Darcy’s law (Darcy 1856). This model was used to determine whether upward movement of water was possible because of capillary forces in the unsaturated soil. In addition, the depth of water uptake was inferred using another 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.
METHODS

Study site

The TTEE is located in the Floresta Nacional do Tapajós (FNT), 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). The study area is a flat terrain of old-growth forest with a continuous canopy, and can be accessed from the Santarém-Cuiabá road (Figure 1). The dry season occurs from June/July to December. From 1999 to 2002, the average annual rainfall falling in the northern part of the FNT was 2110 mm (mean from three sites within the reserve); December 2001 was the driest month (3 mm) while April 2002 was the wettest month (550 mm). The mean annual rainfall according to historical records from the nearby city of Santarém (1914-1981; www.worldclimate.com) is 2061 mm (Figure 1). Nepstad et al. (2002) reports an average rainfall of 2000 mm/year, with a minimum of 600 mm and a maximum of 3000 mm, while Parrotta et al. (1995) reports an average rainfall of 1920 mm/year. The mean monthly temperature is ~25°C (Richards 1996, Parrotta et al. 1995).

The TTEE consists of two 1-ha plots with similar topography, structure, diversity, floristics, biomass 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 ~100m deep (Nepstad et al. 2002). The treatment plot is covered with plastic panels, 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 one-year calibration period (1999) in which both plots were closely monitored to define pre-treatment conditions (Nepstad et al. 2002). In order to avoid lateral infiltration of soil water, a trench 1 m wide x 1.7 m deep has been 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 have been shown to prevent water infiltration from the outside to a depth of at least two to three meters (Nepstad et al. 2002, L. Sternberg, pers. comm.).

**Irrigation design and study species**

The first irrigation experiment started on January 7, 2002, and the second on May 16, 2002. These months correspond to the beginning and end of the wet season, respectively. For these experiments, I selected three tree species shared by both plots: *Coussarea racemosa* A. Rich. (“caferana”, Rubiaceae), *Sclerolobium chrysophyllum* Poepp. (“taxi vermelho”, Fabaceae s.l.), and *Eschweilera pedicellata* (Rich.) S. A. Mori (“mata-matá liso”, Lecythidaceae). The species were selected beforehand from a preliminary hardcopy list of the trees DBH ≥10 cm in the plots (Nepstad et al., unpublished data). There were no special criteria to select these species other than their apparent abundance in this terra-firme forest, according to the printed list. Subsequent analysis, completed after the first irrigation experiment, showed that *C. racemosa* is the most common tree species in both plots, *S. chrysophyllum* is the third most common shared species, and *E. pedicellata* is the seventh most common shared species (Nepstad et al., unpublished data). In addition, *C. racemosa* is typically an understory tree when adult (height ≤10 m) while *S. chrysophyllum* (usually 15–20 m tall) and *E. pedicellata* (generally 10–15 m tall) are understory to mid-canopy trees (Nepstad et al., unpublished data).

In each of the two experiments, five trees of each species were irrigated in each plot (Table 1). The same individual trees in the treatment plot were used for both the first (January 7) and second irrigation (May 16) experiments because I predicted (erroneously) that the January label will disappear from the soil by May, before the second irrigation experiment started. This prediction was supported by the observation that a very large amount of deuterium in the treatment plot was lost in less than one month after the January irrigation, and that there seemed to be little migration of the label in that plot. However, contrary to this expectation, the January label did not disappear from the soil by May (see Figure 4) and it actually was overridden by the May label (see small second peak at ~40 cm depth in Figure 6). In any case, this superimposition of the January and
May labels did not affect the data interpretation because as long as there is a clear non-
convoluted deuterium profile in the soil, the depth of water uptake can be effectively
estimated.

I randomly selected adult trees having DBH ≥10 cm, but, in order to sample the
same number of individuals of each species, I occasionally had to select individuals <10
cm DBH when there were no more adult trees available. If a tree in the treatment plot
grew within 5 m of a very large tree (DBH >1 m), it was not selected because stem flow
from the large tree could overwhelm the throughfall exclusion treatment.

In each irrigation experiment, eight liters of deuterated water (δD = ~130,000 ‰),
prepared in the field by mixing 99% D₂O with local water, were evenly sprinkled around
the trunk of each tree on a circular area of soil with a radius of 1.5 m. Most of the
absorbing roots of adult small trees are apparently located within this radius (Sanford and
Cuevas 1996, Sternberg et al. 2002). The litter around each tree was removed before the
irrigation in order to ensure percolation of the deuterated water into the soil profile. Once
irrigated, the litter was replaced. No extra water was added to push the label deep as this
would have affected the throughfall exclusion treatment. The eight liters of deuterated
water represent 1 mm of rain per unit area. 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 (January 7, day zero) was traced by collecting soil
and plant samples in both plots on day two (but no wood cores of *C. racemosa* were
taken on this day), day five (but no soil cores and no wood cores of *C. racemosa* were
taken on this day), day eight, and day 17. In the control plot, soil and plant samples were
also taken on day 130 (day 128 for the soil cores), day 156 and day 281. The label of the
second irrigation (May 16, day zero) was traced by collecting soil and plant samples in
both plots on day six, day 27 and day 152. Background deuterium levels were assessed
by sampling plant stems and soil cores in a nearby area of forest (“Pique” site). Plant
stems from Pique were collected on January 9 (n=7 stems), January 12 (n=3), January 24 (n=10) and May 22 (n=6), while soil cores from Pique, to a depth of at least 80 cm, were taken on January 8 (n=3 cores) and January 24 (n=1).

At each sampling date, the soil from two to six randomly selected irrigated areas was sampled using a manual auger (one soil core per area). A soil core consisted of soil samples (~7 to ~26 g of wet soil) taken at the surface and then at every 20, 25 or 50 cm depth interval. These samples were taken to below the expected depth of the deuterium pulse at the time of collection. I collected the soil samples in clear screw-cap glass vials and sealed them immediately with Parafilm M® to avoid any isotope fractionation process because of evaporation (Criss 1999).

Stems (~8 cm long and ~8 mm diameter) and wood cores (~5 cm long and ~5 mm diameter) were collected from *C. racemosa*, whereas only wood cores were collected from *S. chrysophyllum* and only stems from *E. pedicellata*. The wood cores were taken at breast height. Stems of *S. chrysophyllum* were too high to reach from the ground, and the very dense hardwood of *E. pedicellata* prevented the manual sampling of wood cores. Several *C. racemosa* stems of the required size were not fully suberized at the time of collection (i.e. they did not present visible cork on surface of stem). Stems and wood cores were collected in vacutainers (13x100 mm) that were sealed with a rubber cap and Parafilm M®. Because the samples were transported via airplane, the air in the vacutainers was evacuated with a syringe to reduce the air pressure.

Soil and plant samples were shipped to the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (University of Miami, USA) or to the Centro de Energia Nuclear na Agricultura (Universidade de São Paulo, Brazil) for analysis. Once they arrived, the samples were stored in a freezer at –10 ºC.

**Water extraction and deuterium measurements**

Procedures for water extraction and measurement of deuterium concentration follow Moreira et al. (2000) and Sternberg et al. (2002). Samples were first thawed overnight to ambient temperature (20 ºC) and then placed in a cryogenic vacuum distillation system. Water collected in this manner was stored in small scintillation vials
with water-proof caps. The hydrogen from the water was extracted using a modified version of Coleman et al. (1982) method: (1) Three µL of water were mixed in an ampoule with 150 mg of zinc previously outgassed at 350 ºC for ten minutes, (2) the ampoule was frozen in liquid nitrogen and sealed under high vacuum, (3) hydrogen gas was produced by placing the ampoule in an oven for two hours at 500 ºC. The deuterium content of the hydrogen sample was analyzed using a Micromass Prism dual inlet isotope ratio mass spectrometer (model Finnigan Delta X). The average spectrometer precision for each sample analyzed was ± 0.14 δD units.

The concentration of deuterium in the hydrogen was expressed in δD values. These represent the relative difference per mil (‰) between the isotopic composition of a sample and the isotopic composition of an international standard, in this case SMOW (Standard Mean Ocean Water; Craig 1961). The isotopic composition is expressed as the atomic ratio (R) of ‘heavy’ isotopes to ‘light’ isotopes, in this case deuterium hydrogen (²H or simply D) to protium hydrogen (¹H or simply H): D/H.

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

Data analysis and models

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. I developed a MATLAB® program which calculated the expected δD values for every centimeter in the soil profile via cubic spline interpolation based upon the observed mean δD values. I used this program to calculate the 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®. Data from the January 9 sampling (day 2 after the first irrigation) was not graphed because the soil cores on that day were taken only to 20 cm depth. Soil water in the irrigated areas at any depth was considered enriched when it was above the highest background value of the Pique site (δD = -12‰).
The data from the second irrigation of the treatment plot were treated as if the treatment plot had no panels on May 22 and June 12, although the panels were not actually removed until July 1. I analyzed the data this way because the amount of throughfall under the panels in the treatment plot from May 22 to July 1, a transitional period between the wet and dry seasons, was not significantly different from the amount of throughfall in the control plot during this same period (two-tailed t test: \( t = 1.56, P = 0.12, n = 40 \) days). The second irrigation experiment is therefore denoted in this study as the ‘dry season’ experiment, although it actually started in mid-May.

In addition, the depths of peak deuterium concentration were correlated with the amount of throughfall accumulated over time in the presence and in the absence of panels. This analysis helped to understand how the amount of rain reaching the soil affects the vertical movement of water in the soil.

Plant samples

I used a one-tailed t test to evaluate if the \( \delta D \) values of the plant samples at each date were significantly higher than background deuterium levels defined by the Pique stem samples. Because no Pique samples were collected on June 12 and October 15, I used the May 22 Pique data as the background control for these dates.

Only the data from the wood cores of *S. chrysophyllum*, the wood cores of *C. racemosa* and the stems of *E. pedicellata* were analyzed. I did not analyze the \( \delta D \) values of the stems from *C. racemosa* because they were taken at different heights in the trees and because some that were not completely suberized may have been enriched by evaporation of the stem epidermis (Dawson and Ehleringer 1993). I had to use stem data for *E. pedicellata* because they were the only available.
Model of soil water movement

I developed a basic model —written in MATLAB® (Appendix 1)— which simulates the movement of water in the unsaturated or vadose zone of clay soils. This model considers the effect of precipitation, water uptake (i.e. transpiration and root distribution), matric potential, gravitational potential and hydraulic conductivity on the movement of soil pore water in a stratified one-dimensional column of soil. All these variables were modeled using algorithms that simplify the actual processes in nature. Further, surface runoff was not modeled, and soil evaporation beneath and at the surface was assumed to be zero (an unrealistic assumption). Given the simplifying nature of the model, I did not use it to simulate the water content dynamics or the actual observed pattern of water movement in the soil (the movement of the deuterium label already describes this), but to understand the relationship between rainfall and capillary movement of water in clay soils during wet and dry seasons given an initial input of water content at every depth and a continuous input of throughfall over time (input was actual real data). Specifically, I investigated if the model would simulate upward movement of water solely because of inherent physical characteristics of the soil. The model was developed as follows:

1. The soil was assumed to be physically homogeneous at all depths (i.e. as an ideal continuum medium where descriptive physical parameters of the soil such as maximum and minimum saturation, pore size distribution, air entry value and saturated hydraulic conductivity are constant). This assumption does not fit to reality, particularly at shallow depths (<2 m) where the presence of roots and fauna probably create a very heterogeneous environment. The soil column was also evenly stratified into “cells” of the same height (constant spatial discretization; Figure 2). Note that the cells represented in Figure 2 have two dimensions (height and width) for graphical representation purposes and ease of understanding only. The actual modeled movement of water is in one dimension only (the vertical z axis), not in two dimensions.

2. To describe the movement of soil water in the soil column through discrete time, I used a modified version of the water balance equation presented by Guswa et al. (2002) (one of the signs, probably a typo, was changed). This equation is based on a
solution of the Richard’s equation (Richards 1931) and Darcy’s law (Darcy 1856), where
the water content of cell $i$ at time $t+1$ is equal to:

$$\Theta_{i}^{t+1} = \Theta_{i}^{t} + P_{i} - E_{i}^{t} - U_{i}^{t} + \Delta t \left[ K_{i+\frac{1}{2}} \left( \frac{h_{i+1} - h_{i}}{\Delta z} - 1 \right) + K_{i-\frac{1}{2}} \left( \frac{h_{i-1} - h_{i}}{\Delta z} + 1 \right) \right]$$  \hspace{1cm} (2)

where $\Theta_{i}$ is the water content of cell $i$, here expressed in mm, not as a volume fraction; $P_{i}$ (mm) is the amount of precipitation reaching cell $i$; $E_{i}$ (mm) is the amount of water evaporated from cell $i$ (soil evaporation), here assumed to be zero; $U_{i}$ (mm) is the amount of water from cell $i$ taken up by the plants; $K$ (mm hour$^{-1}$) is the unsaturated hydraulic conductivity ($K_{i+\frac{1}{2}}$ or $K_{i-\frac{1}{2}}$ is the unsaturated hydraulic conductivity between two consecutive cells, obtained by averaging the $K_{i}$ of two adjacent cells); $h_{i}$ (mm) is the soil matric potential of cell $i$ expressed in pressure heads of water and is negative; $\Delta z$ (mm) is the thickness of the cell, representing the elevation difference (gravitational potential).

The water content in mm (a one dimension unit) was calculated from the volumetric water content, which is the portion of pore volume filled with water in a volume unit of soil (i.e. in a three-dimensional cubic cell), measured in the field using time-domain-reflectometry techniques (TDR). The relatively short units of time (hour) were used because the program algorithms are more stable with small time intervals. I use mm as the unit of length because it is commonly used in measurements of precipitation and water uptake.

3. The unsaturated hydraulic conductivity ($K$) and the matric potential ($h$) were calculated from the equations developed by van Genuchten (1980), further explained by van Genuchten et al. (1991). I used these equations because they have been successfully used in a study in the central Amazon (Tomasella and Hodnett 1996). These equations describe the hydraulic relationships between $\Theta$, $K$ and $h$ in an unsaturated soil (i.e. the water retention curve). The matric potential was calculated by solving for $h$ in the following equation (van Genuchten 1980):

$$S_{e} = \frac{\Theta_{e} - \Theta_{r}}{\Theta_{s} - \Theta_{r}} = \frac{1}{1 + (\alpha h_{r})^{n}} \hspace{1cm} (m = 1 - 1/n)$$  \hspace{1cm} (3)
where $S_e$ is the effective degree of saturation ($0 \leq S_e \leq 1$) in cell $i$; $\alpha$ is an empirical parameter (mm$^{-1}$) whose inverse can be referred to as the air entry value or bubbling pressure; and $n$ and $m$ are empirical constants which, together with $\alpha$, affect the shape of the water retention curve (van Genuchten et al. 1991). $\Theta_r$ and $\Theta_s$ are the residual and saturated water contents, respectively. $\Theta_r$ and $\Theta_s$ are theoretical constants of the soil water retention functions that are difficult to measure in practice (van Genuchten et al. 1991). $\Theta_r$ specifies the maximum amount of water in a soil that will not contribute to liquid flow because of blockage or strong adsorption onto the solid phase (van Genuchten et al. 1991). $\Theta_r$ can formally be defined as the water content at which both $d\Theta/dh$ and $K$ go to zero when $h$ becomes large, which means that $\Theta_r$ is an extrapolated parameter and thus may not necessarily represent the smallest possible water content in a soil (van Genuchten et al. 1991). $\Theta_s$ is simply the maximum water content that a unit of soil can hold at a given time, but should not be equated to the porosity which can be 5–10% larger than $\Theta_s$ because of the presence of entrapped or dissolved air (van Genuchten et al. 1991). The definition problem for $\Theta_r$ and $\Theta_s$ is similar to that for the terms "permanent wilting point" and "field capacity" — they are conceptually useful for understanding plant water relations, but they lack an exact physical definition (Taiz and Zeiger 1991, Marshall et al. 1996).

By making $m=1-1/n$, van Genuchten (1980) simplified the Mualem (1976) model to estimate the unsaturated hydraulic conductivity of a cell as a function of the matric potential in a porous medium:

$$K(h_i) = \frac{K_s \left\{1 - (\alpha h_i)^m \left[1 + (\alpha h_i)^n \right]^m \right\}^2}{\left[1 + (\alpha h_i)^n \right]^{m\ell}} \quad (m=1-1/n) \quad (4)$$

where $K_s$ is the saturated hydraulic conductivity and $\ell$ is the pore-connectivity parameter related to the tortuosity (van Genuchten 1980, van Genuchten et al. 1991, Tomasella and Hodnett 1996). For computational convenience, $h$ is positive in equations 3 and 4, but $h$ is negative to calculate the water content of a cell in equation 2. At every time interval, a new $h$ is calculated for each cell. This $h$ is then used to calculate a new $K$ for each cell. Both $h$ and $K$ ultimately depend on the effective saturation at different depths in the soil.
As mentioned before, to calculate the water movement, the $K$ between two contiguous cells ($K_{i+1/2}$ or $K_{i-1/2}$) must be calculated by averaging the $K_i$ of those cells (see equation 2).

4. The amount of precipitation reaching cell $i$ at time $t$ ($P^t_i$) was modeled by assuming that no precipitation was lost by surface runoff. A cell will be filled with rain water until it reaches saturation ($\Theta$); the remaining precipitation will then pass to the cell below it. Water will keep percolating downwards in the soil until no precipitation is left. This process was repeated for each time interval characterized by a given precipitation.

5. The amount of water taken up by plants from a cell $i$ at time $t$ ($U^t_i$) was modeled assuming: a) a maximum and constant transpiration value, here assumed to be equal to the mean evapotranspiration in these forests, i.e. $\sim$4 mm/day (Leopoldo et al. 1995, Hodnett et al. 1996, Jipp et al. 1998, Costa and Foley 1999, Potter et al. 2001), and b) constant spatial distribution and abundance of fine roots ($<2$ mm diameter) over time. Relative fine root distribution was assumed to be the same as the relative total root distribution and it was described using a mean cumulative root fraction function for tropical evergreen forests (Jackson et al. 1996):

$$Y = 1 - 0.962^d$$

(5)

where $Y$ is the cumulative root fraction (maximum=1) and $d$ is depth (cm). Therefore, the proportion of roots present in a given cell ($R_i$) that could potentially take up water is given by:

$$R_i = (1 - 0.962^{d+1}) - (1 - 0.962^d) = 0.962^d - 0.962^{d+1}$$

(6)

where depth must be in cm. $R_i$ is not the proportion of roots at a given depth —which would be equal to $0.036(0.962^d)$— but is the proportion of roots in a whole cell (i.e. in the depth range from the top to the bottom of a cell). The summation of $R_i$ at all depths equals one.

The amount of water harvested from a cell was set equal to the maximum transpiration only if the cell was fully saturated ($S_e=1$). This accounts for a root absorbing water proportionally to the water content in the soil. If the water content drops below a
certain limit, in this case $\Theta_r$, water uptake ceases completely because of lost of physical contact and/or strong adsorption of the water to the solid matrix (see Plamboeck et al. 1999). This can be expressed as:

$$U'_i = (R_i T)S_e$$  \hspace{1cm} (7)

where $U_i$ (mm) is the amount of water taken by the plants from cell $i$ at time $t$, and $T$ is transpiration at time $t$ (equal to 4 mm/12 daylight hours = 0.33 mm/daylight hour; in the night, when $T$ is assumed to be zero, there is no water uptake).

6. In order to program the temporal and spatial dynamics of soil moisture movement in MATLAB®, the equations describing the movement of water in each cell (Figure 2) were transformed to a matrix/vector equation (see van Genuchten and Sudicky 1999, Sternberg and DeAngelis 2002). The transient terms in the set of equations that relate the water table to the lowest depth of the soil column (Figure 2) were eliminated because the water table is very deep at this site (100 m; Nepstad et al. 2002) and therefore has a minimal impact on the soil moisture dynamics of the upper soil layers (Eagleson 2002, Guswa et al. 2002, F. Miralles-Wilhelm, pers. comm.). Applying a similar logic, the terms that describe the boundary between the soil and the atmosphere were also excluded. Therefore, in this model, the matrix/vector equation that describes the movement of water at time $t+1$ after a discrete time interval ($\Delta t=1$ hour), for a soil column example of four cells (Figure 2), takes the following form:

$$
\begin{bmatrix}
\Theta_1 \\
\Theta_2 \\
\Theta_3 \\
\Theta_4 \\
\end{bmatrix}^{t+1} = 
\begin{bmatrix}
\Theta_1 \\
\Theta_2 \\
\Theta_3 \\
\Theta_4 \\
\end{bmatrix}^t + 
\begin{bmatrix}
P_1 \\
P_2 \\
P_3 \\
P_4 \\
\end{bmatrix} 
\begin{bmatrix}
U_1 \\
U_2 \\
U_3 \\
U_4 \\
\end{bmatrix} - 
\begin{bmatrix}
-K_{15} & +K_{15} & 0 & 0 \\
K_{15} & (-K_{15}-K_{25}) & +K_{25} & 0 \\
0 & +K_{25} & (-K_{25}-K_{35}) & +K_{35} \\
0 & 0 & +K_{35} & -K_{35} \\
\end{bmatrix} 
\begin{bmatrix}
h_1/\Delta z \\
h_2/\Delta z \\
h_3/\Delta z \\
h_4/\Delta z \\
\end{bmatrix} + 
\begin{bmatrix}
-K_{15} \\
(+K_{15}-K_{25}) \\
(+K_{25}-K_{35}) \\
+K_{35} \\
\end{bmatrix}
$$

(8)

where all the terms are positive, except $h$ which is negative (see equation 2).

7. The purpose of the model is not to explore the hydraulic relationships among $K$, $h$ and $\Theta$, but to model the movement of water in a soil column using simple assumptions. Therefore, soil evaporation ($E$) was set to zero, and $\Delta z$ (= 200 mm) together with $\Delta t$ (= 1
hour) were kept constant (uniform spatial and temporal discretization). I arbitrarily set $\Theta_r$ to 20 mm (TDR value or volume fraction = 0.1) and $\Theta_s$ to 120 mm (TDR = 0.6) for all the cells (see equation 3). This range permitted stable performance of the model algorithms over time. $\Theta_r$ in this model is lower than the minimum TDR value recorded in the study plots (0.15, equivalent to 30 mm of water for a cell height of 200 mm), while $\Theta_s$ is higher than the maximum observed TDR value (0.48, equivalent to 96 mm of water) (Nepstad et al. 2002, and more recent unpublished data). For clay soils, the lowest volume fraction published for $\Theta_r$ is 0.068 (van Genuchten et al. 1991) while the highest is 0.59 (Tomasella and Hodnett 1996). The other van Genuchten parameters used in this model ($K_s$, $\alpha$, $n$, $\ell$) were kept constant at all depths. I averaged the $\alpha$ and $n$ values (see equations 3 and 4) reported by Rawls et al. (1982) and Carsel and Parrish (1988) for clay soils, as summarized by van Genuchten et al. (1991) (Table 2). I set $K_s$ (see equation 4) to 550 mm/hour, the average from all the estimated $K_s$ at different depths in a soil near Manaus (Tomasella and Hodnett 1996). The $\ell$ parameter (see equation 4) was fixed to 0.5 as recommended by Mualem (1976). A recent study (Hodnett and Tomasella 2002) provides updated mean values for the van Genuchten parameters for tropical soils, but I became aware of their publication only after my simulations had been completed. For clay soils, they propose mean values of 0.267, 0.546, 0.00463 and 1.514 for $\Theta_r$, $\Theta_s$, $\alpha$ and $n$, respectively. These are very similar to the values I used (Table 2).

Soil water movement was simulated six times (six different outputs) corresponding to six consecutive wet and dry seasons from January 2000 to December 2002. The seasons were assumed to last half a year, a good approximation of the seasonal pattern at the site (Figure 1). Thus, for modeling purposes, a wet season lasted from January 1 to June 30, while a dry season lasted from July 1 to December 31. The initial measurements of water content at different depths were interpolated from TDR measurements taken in the field within thirty days from the first day of each season, either January 1 or July 1 of each year (Nepstad et al., unpublished data). The precipitation input was corrected for canopy interception (i.e. it was input as throughfall, which in this forest is ~80% of the precipitation; Nepstad et al. 2002). The maximum depth of the soil column was set to 5 m (5000 mm), the lowest depth for which I had available data of water content measurements. The water content for each cell in the soil
column was interpolated from TDR measurements taken at 0.3, 0.5, 1, 2, 3, 4 and 5 m (Nepstad et al. 2002). For analysis and graphing purposes, the model output for each hour was summarized as 24-hour periods to represent the amount of water (mm) moving upwards in one day.

Model to determine mean depth of water uptake by plants

To estimate the mean depth of water uptake by an individual plant, the δD values in the soil profile and the δD value of sap water in a tree were coupled in another model. As input, this model uses the soil/plant data from those sampling dates in which treatment and control plots had plant δD values significantly above background. Samples from days two, five, and eight after the first irrigation and day six after the second irrigation were not analyzed because (1) in the first irrigation experiment, no wood cores of C. racemosa were collected on days two and five, and no soil samples were collected on day five, and (2) data collected on these days do not provide reliable information on the depth of water uptake. These data may be unreliable because (1) no equilibration of the deuterium concentration in the soil-plant continuum had probably yet been attained, and (2) the label probably had not fully migrated from the soil to the trunk/stems of the trees. This last reason is supported by the fact that, depending on the season and the plot, it takes at least three to five days for the deuterium to migrate from the upper soil layers to the height in the tree where the wood cores/stems were taken (Nepstad et al. unpublished data). Further, during the throughfall exclusion period (wet season), the average sap flow rate of the trees in the treatment plot is ~50% slower than the sap flow rate of the trees in the control plot (Nepstad et al. unpublished data). Therefore, given all these possible confounding factors on data interpretation, for the depth of water uptake analysis I only used the soil and plant data from 17 days (January 24) after the first irrigation and from 27 days (June 12) and 152 days (October 15) after the second irrigation.

This model —written in MATLAB® (Appendix 2)— was developed with the following assumptions and premises:

1. I assumed that at a given time, a tree can take up water from a vertical segment of soil that is 50 cm long and which can be localized at any depth in the soil profile. The following reasoning was used to support this assumption. During three years 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, while the minimum average was 0.25 (Nepstad et al. 2002, Nepstad et al. 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. Because daily evapotranspiration in these forests is on the average ~4 mm/day at any point in the forest (Leopoldo et al. 1995, Hodnett et al. 1996, Jipp et al. 1998, Costa and Foley 1999, Potter et al. 2001), every day plants must acquire water from a vertical segment of soil of at least 4 cm long. There may be differences in the length of the soil segment used by different species of trees to harvest water, especially between the 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) is seven days. In order to sustain the transpiration demand during those seven days when no precipitation falls and the soil is not recharged with water, plants must be able to extract water from at least 28 cm of soil (4 cm soil/day x 7 days). 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/day x 25 days) to sustain transpiration. The length of the vertical soil segment used in this study, 50 cm, falls within the range of these estimates and is a conservative approximation. Any error in my 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 just a ~10% change in model output (i.e. in the calculated mean depths of water uptake).

2. I 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 (Figure 3; Sokal and Rohlf 1995):
$n_i = \frac{1}{\sigma \sqrt{2\pi}} e^{-(Y-\mu)^2/2\sigma^2}$ (9)

where $n_i$ is the proportion of water taken up at a depth $Y$, and $\mu$ 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 so that they always summed to one by weighing them by the area under the curve. 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 (Figure 3). I assumed that a tree takes up water from a 50 cm segment of soil, therefore the standard deviation ($\sigma$) of this normal distribution is approximately equal to 8.33 cm and the mean ($\mu$) is the mean depth of water uptake. In the model, a plant actually absorbs only 4.8% of the water from the mean depth ($n_i = (1/8.33\sqrt{2\pi}) \times e^0 = 0.0478$; Equation 9); the other 94.9% ($=99.7-4.8$) of the water comes from the other depths in the 50 cm soil segment.

I 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, Flanagan et al. 1992, Dawson and Pate 1996, Lin et al. 1996, Schwinning et al. 2002).

3. A premise supported by mass balance principles is 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 the sum of the deuterium signatures of 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 (Equation 9). This can be expressed as (Moreira et al. 2000):

$$\delta D_{c, \text{plant}} = \sum_{i=1}^{m} (n_i \times \delta D_{i, \text{soil}})$$ (10)
where $\delta D_{\text{plant}}^c$ is the calculated hydrogen isotopic composition of plant stem/trunk water, $n_i$ is the proportion of water uptake at the $i$th depth relative to the water uptake at all depths in the 50 cm segment of soil, and $\delta D_{\text{soil}}^i$ is the isotopic composition of soil water at the $i$th depth (an average value in this study). The model compares the $\delta D_{\text{plant}}^c$ value to the observed $\delta D_{\text{plant}}^o$ which is the $\delta D$ value of the actual plant water sample measured in the lab.

For a given deuterium profile in the soil, an infinite number of $\delta D_{\text{plant}}^c$ is possible, each with a corresponding mean depth ($\mu$) of water uptake. For a given mean depth, the difference between $\delta D_{\text{plant}}^c$ and $\delta D_{\text{plant}}^o$ could be positive or negative, depending whether $\delta D_{\text{plant}}^c$ is greater or lower than the $\delta D_{\text{plant}}^o$. Only those mean depths at which $\delta D_{\text{plant}}^c$ is equal to $\delta D_{\text{plant}}^o$ are considered solutions, i.e. a solution is possible only when the difference between $\delta D_{\text{plant}}^c$ and $\delta D_{\text{plant}}^o$ is zero. The program shifts the 50 cm soil segment of water uptake deeper and deeper in the soil profile by one cm increments, calculating at the same time a mean depth of water uptake for every position of the 50 cm segment. Then, all the mean depths at which the difference between $\delta D_{\text{plant}}^c$ and $\delta D_{\text{plant}}^o$ is zero are saved as solutions.

In some cases, assuming a soil segment of water uptake 50 cm long, no solution was possible, i.e. $\delta D_{\text{plant}}^o$ did not match any $\delta D_{\text{plant}}^c$ at any depth. I excluded these trees from the water uptake analysis. The effect of their exclusion is probably minimal because they represent only 11% of the total number of samples analyzed (total=90 samples). On the other hand, in 9% of the plant 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, I averaged these mean depths of water uptake and treated them as a single observation for data analysis purposes. Solutions with values >3 m were excluded from the analysis because such depths were not yet enriched by the deuterium label at the time of sampling. More solutions are mathematically feasible if the shape of the deuterium profile in the soil is convoluted, i.e. showing the same $\delta D$ values at different depths. Such complex patterns occur naturally in the Amazon, and this is why the
addition of an enriched label to override any convoluted pattern is justified (Moreira et al. 2000, Meinzer et al. 2001). Certain depth(s) may appear as a solution(s) only if a certain standard deviation (i.e. length of the soil segment of water uptake) is used. If no solution is possible with any standard deviation, then the plant’s δD cannot be explained by the observed distribution of the deuterium in the soil (at least not with this model), and the plant is probably taking up water below the lowest depth analyzed.

In summary, the model I used to estimate the mean depth of water uptake (µ) relies on two important assumptions and one premise: (1) at a given time, trees take up water from a 50 cm vertical segment of soil, (2) the amount of water taken up at every cm in the soil segment follows a normal distribution, and (3) the deuterium signature in a plant sample is equal to the sum of the deuterium signatures of the soil water absorbed by the plants at different depths. 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 label percolated downwards at a mean rate of 0.75 m/month in the control plot, and 0.07 m/month in the treatment plot (Figure 4). On May 15 (128 days after the first irrigation), the deuterium peak in the control plot had reached a depth of 254 cm while in the treatment plot the peak had only reached a depth of 29 cm (Figure 4). During the dry season (starting in June), the deuterium label in the control plot stopped percolating but rather began to move back upwards (Figure 5): by October 15 (281 days after the January irrigation) the deuterium peak rose to a depth of 190 cm (64 cm shallower than the May 15 position; Table 3). In the treatment plot, upward movement of the deuterium label was not observed because the deuterium did not percolate deeply (Figure 4).

Two days after the irrigation, on January 9, the peak deuterium concentration in the treatment plot (average $\delta D \pm$ one standard error of the mean (SEM) = 10,348 ± 2,568; n=7 soil cores) was significantly greater ($P = 0.03$; two-tailed t test) than that in the control plot (average $\delta D \pm$ SEM = 3,427 ± 696; n = 6). The deuterium concentration in both plots decreased over time, and the difference in the peak deuterium concentration between both plots diminished (Figure 4).

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 (~0.15 m/month; Figure 6). Thus, by October 15 (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; Figure 6, Table 3). The depths of these peaks were similar to the depth reached by the peak in the treatment plot during the wet season (29 cm; Figure 4) while the panels were in place simulating a dry season. There was no upward movement of the second label during the dry season in either plot (Figure...
6). As in the first irrigation, the deuterium concentration in both plots decreased over time (Figure 6).

Effect of precipitation on the percolation of deuterium

Downward movement of the deuterium peak was highly correlated with throughfall, regardless of whether or not the panels were present (both $P \leq 0.01$; Figure 7). This correlation was strengthened by the inclusion of four data points (represented as triangles in Figure 7) obtained from another deuterium irrigation experiment conducted in the same site (next to the TTEE plots) which lasted from March 1999 to January 2000 (Sternberg et al. 2002). In the absence of panels—a condition common to both plots during the dry season—rain pushed the label at a rate four times greater than in the presence of panels (slopes: 1.88 vs. 0.45; Figure 7). At any time, the depths of peak deuterium concentration in the control plot and in the treatment plot without panels were approximately twice the amount of cumulative throughfall (slope=1.88; Figure 7). For example, after the accumulation of 20 cm of rain, the deuterium peak was approximately 40 cm deep. On the other hand, the depth of the deuterium peak in the treatment plot when the panels were in place was approximately half the amount of accumulated throughfall (slope = 0.45; Figure 7).

Output of the model of soil moisture movement

The upward movement of water observed in the deuterium label during the dry season (Figure 5) was also observed in the model simulation (Figure 8). Most upward water movement occurred during the dry seasons, although some water also moved upwards during the wet seasons (Figure 8; Table 4). There is a clear inverse relationship between rainfall intensity and the amount of water that subsequently moves up: more water moves up during the dry seasons, particularly at depth. For example, the model shows that more water moves up at 4 m than at 2 m (Table 4).

Patterns of plant enrichment and mean depths of water uptake

$\delta D$ of sap water from all tree species in both plots were significantly above background 17 days after the first irrigation and 27 days after the second irrigation (Table
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 days after the first irrigation in the control plot, and three *C. racemosa* control trees (9-164, 9-189, 9-201; see Table 1) became significantly enriched again in October after being at background levels since at least May 17 (*P* < 0.001, Z test using the June 12 mean background \(\delta D\) value, -41.2, as the population mean). The enrichment of these three trees increased the mean \(\delta D\) of all five *C. racemosa* trees to -15.2, but this mean was not significantly higher than the mean of the background control data from the Pique site (Table 3).

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, on a given date, were significant or almost significant for all three species (two-tailed t test; Figure 9). On January 24, 17 days after the first irrigation and 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 (Figure 9). This pattern reversed on June 12 (beginning of the dry season, 27 days after the second irrigation) and October 15 (mid-dry season, 152 days after the second irrigation), when the trees in the treatment plot were taking up water at deeper depths than the trees in the control plot (Figure 9). On the average, on June 12 and October 15, trees in the treatment plot harvested water at a depth 26 cm and 37 cm deeper than the trees in the control plot, respectively (Figure 9). As the dry season progressed from June to October, the trees in both plots tended to take up water at greater depths (Figure 9).
DISCUSSION

Rain regulates the percolation of water in the soil profile, but capillary forces can move water upwards.

The throughfall exclusion treatment had a major effect on the percolation of water through the soil profile (Figure 4). During the 2002 wet season, the percolation rate in the control plot (0.75 m/month) was much higher than that in the treatment plot (0.07 m/month), confirming the first postulate. The percolation rate in the treatment plot in the wet season, when the panels were in place, was even lower than the rate in the dry season, when the water in both plots percolated at the same rate (0.15 m/month; Figure 6). These rates are within the range published in the literature for humid tropical forest soils (Kline and Jordan 1968, Aragúas-Aragúás et al. 1995, Moreira et al. 2000, Sternberg et al. 2002), although the 2002 wet season percolation rate in the control plot may well be the highest ever reported (0.75 m/month). The similar dry season percolation rates (Figure 6) suggest that the physical characteristics of the soil are alike in both plots, and that the main factor regulating the downward movement of water in the plots is rain input (Aragúas-Aragúás et al. 1995, Moreira et al. 2000, Sternberg et al. 2002). This relationship is linear and highly significant: under natural conditions (no panels), every centimeter of rain “pushes” the soil water a distance of about two centimeters (slope = 1.88, $P<0.0001$, Figure 7). This 1:2 relationship can be explained by assuming that, in this forest, ~50% of a volume unit of clay soil is water, while the other 50% is either solid matter or entrapped air (the maximum $\Theta$, recorded in the plots is just below 0.5; Nepstad et al. 2002), which means that one centimeter of rain can only fit in the soil column if the water from two centimeters of soil is displaced. If the three cumulative throughfall values >100 cm are excluded from the correlation (see Figure 7), the correlation is still significant and the 1:2 relationship is maintained (slope = 2.28, $r = 0.928$, $P <0.001$).

Water in the soil profile at depths >2 m can move upwards several decimeters during a dry season (Figure 5). A similar pattern was also found in a seasonal forest and abandoned pasture in the eastern Amazon (Moreira et al. 2000, Sternberg et al. in prep.) confirming this phenomenon. From the end of the wet season (May 15) to the middle of
the dry season (October 15), the deuterium peak on the average moved up from 254 cm to 190 cm (Figures 4 and 5; Table 3) which—assuming that the 1:2 relationship described previously (Figure 7) is applicable in this situation as well—means that 32 cm of water moved up.

Upward movement of water can be explained by (1) the tortuous capillary nature of tropical clay soils (e.g. Prathapar et al. 1992, Marshall et al. 1996), or by (2) the redistribution of water (hydraulic lift) by plant roots (e.g. Richards and Caldwell 1987, Dawson 1993). In this study, however, the upward movement of water is not likely to be explained by hydraulic lift. If roots were absorbing water from moist (deep) soil layers and depositing it in dry (shallow) soil layers, the deuterium soil profile should reflect this process. If hydraulic lift occurred by roots taking up water at 2.5 m depth and then depositing it at 2 m night after night, the October 15 deuterium profile should show a second peak around 2 m (Figure 10) because in general there is no isotopic fractionation by plant roots (Gonfiantini et al. 1965, Wershaw et al. 1970, but see Lin and Sternberg 1993). Alternatively, if hydraulic lift occurred gradually throughout the soil profile, as expected if the root distribution is continuous, then the deuterium profile curve should exhibit an extended tail (Figure 10). Neither of these possible deuterium profiles was observed in this study and therefore I suggest that, in tropical forests, large amounts of water can move upwards because of the tortuous capillary nature of clay soils (first explanation above), especially if little or no rain falls for a relatively long period of time.

In fact, the model of soil water movement shows that upward movement of water (Figure 8, Table 4), in a physically homogenous column of clay soil, (1) can occur because of capillary forces alone, (2) is typically more intense during dry seasons than during wet seasons, and (3) is pronounced at depth (because the soil water content is higher at greater depths). The phenomenon of capillary rise (upward water movement) in clay soils, up to several meters, is well described in the soil physics and agricultural literature, although it mostly has been related to the presence of a shallow groundwater table (e.g. Brouwer et al. 1985, Malik et al. 1989, Prathapar et al. 1992, Marshall et al. 1996).

The total amount of water predicted by the model to move upwards in a dry season (Table 4), however, is very small compared to what the deuterium label shows (~32 cm of water, or a distance of 64 cm, as explained previously; Figures 4 and 5, Table
3). Changes in the values of different input parameters did not substantially change the pattern and magnitude of upward water movement (data not shown). This disagreement between the model and the deuterium profiles likely reflects model limitations. For example, the model is very sensitive to the time interval and cell height used. If the time-step is too large and/or the cell height is too small, the amount of water calculated to leave a cell could exceed the amount of moveable water contained in the cell and thereby lead to a negative effective saturation ($S_e < 0$) and subsequent mathematical instability. However, if no precipitation is input and water uptake is set to zero, the model smoothly translocates the water until all cells have similar water content. This acceptable performance of the model under steady-state conditions demonstrates that water in clay soils can move up only because of capillary forces (i.e. differences in matric potential and gravitational potential) during a dry season. The model can be perfected by implementing mechanisms of (1) rainfall runoff generation (Eagleson 2002, Guswa et al. 2002), (2) evaporation (Jones 1992, de Rosnay and Polcher 1998, Eagleson 2002, Guswa et al. 2002), and (3) water uptake that incorporates root growth, root absorptive surface, presence of mycorrhizae, and differences in water potential throughout the soil-root-leaf continuum (Jackson et al. 1997, de Rosnay and Polcher 1998, van Genuchten and Sudicky 1999, Jackson et al. 2000a, Jackson et al. 2000b, Feddes et al. 2001, Guswa et al. 2002, Wilderotter 2003).

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, 1967b, Blume et al. 1967, Münnich 1983). At depths >50 cm, evaporation is minimal and therefore the loss of the label must be related to water uptake by plants and dilution by incoming precipitation or local water (Woods and O’Neal 1965, Zimmermann et al. 1966, 1967a, 1967b, 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 two meters depth (e.g. the $\delta^D$ value of the May 15 peak from the first irrigation in the control plot is very similar to the $\delta^D$ values of the June 12 and October 15 peaks; Figures 4 and 5). This leads to the conclusion that plant water uptake at depths >2 m must be minimal (see also Sternberg et al. 2002). Regarding the discussion in the previous section, this is further evidence against the possibility that hydraulic lift was the cause of the upward movement of water in the control plot from ~2.5 to ~2 m depth during the 2002 dry season.

$\delta^D$ of sap water from all tree species in the control plot were significantly enriched as long as soil water close to the surface had $\delta^D$ values above background (Table 3). By May 17, after downward percolation of the deuterium label caused the soil to be above background from 0.84 m to 3.0 m deep, only one species ($E. pedicellata$) had sap water with $\delta^D$ values significantly above background levels (Table 3). None of the species was enriched once further downward percolation of the label occurred and the soil water was above background only at depths >1.42 m (by June 12; Table 3). Therefore, the individuals studied here, some of which had a DBH as large as 20-26 cm (Table 1) 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 depth. This is puzzling when considered in the context of the observed decrease in soil moisture in the control plot down to at least three meters 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 (Nepstad et al. unpublished data). Further, depletion of soil moisture has occurred down to at least 10 m depth in the soil profile of the treatment plot (Nepstad et al. 2002). A possible solution to this problem is the observation of the upward movement of the deuterium label during the dry season (Figure 5), which, as discussed, can be explained by capillarity. Plants may access a substantial amount of deep soil moisture through this route rather than by direct water uptake at depth. Evidence supporting this hypothesis can be seen in the changes of the $\delta^D$ 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, the $\delta^D$ values of sap water from three of the five individuals of $C. racemosa$ were unexpectedly enriched ($Z$ test, $P<<0.001$, see Results).
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 deep 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) (Figure 9). All three species showed this pattern with some species in the treatment plot accessing water as much as ~0.5 m below that accessed in the control plot (Figure 9). 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 to 0.8 m) than during the mid-dry season (0.6 to 1.25 m; Figure 9).

The January sampling (at the beginning of the 2002 wet season) did not conform to my expectations. On average, trees in the treatment plot were actually accessing soil water from shallower layers (0.13 to 0.57 m) of the soil profile than control trees (0.79 to 1.11 m) (Figure 9). The simplest and most probable explanation of this phenomenon is that irrigation with eight liters of deuterated water (1 mm of rain or 32% of the average daily throughfall) around each tree in the treatment plot temporarily moistened the surface layers of the soil profile enough to induce fine root production. The enriched water was sprinkled on a relatively litter-free soil (see Methods), which may have reinforced such an effect. A complementary explanation is that the substantial throughfall between the panels (e.g. 162 mm from January 1 to January 24) plus the flow of water along trunks (stemflow) induced superficial fine root growth around tree trunks from primordia that were probably latent throughout the dry season. As a result, the treatment trees may have quickly switched their strategy from deep to shallow water uptake at the very beginning of the 2002 wet season, before the first irrigation (January 7). In fact, a major increase in fine root production at 50 cm depth in the treatment plot has been observed at the beginning of a wet season (Nepstad et al. 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 (Nepstad et al. unpublished data) but, at least at the very beginning of the wet season, the bulk of water uptake is still apparently occurring at depths of ~1 m (0.79 to 1.11 m on the average; Figure 9). The water at these depths is probably enough to sustain the transpiration demand because it has not been depleted by the exclusion treatment and is being quickly recharged by infiltrating precipitation (de Souza et al. 1996, Nepstad et al. 2002). This could be the situation throughout the wet season, although I lack data to support this speculation. When the frequency and intensity of rains begin to decrease in June (a transitional month between wet and dry seasons), the control as well as the treatment trees eventually conform to the expected trend: control trees tap water at shallower depths than treatment trees because of higher depletion of surface water content in the treatment plot than in the control plot (Figure 9).

Concluding remarks

The lack of difference in the depth of water uptake among the three species studied, belonging to different taxonomical orders, was not anticipated. However, because of this consistent result, the patterns found in this study may accurately represent the physiological response to soil water depletion (“soil drought”) of many other trees in this forest community. The depth of water uptake patterns may reflect similar, species-independent, rooting patterns of understory to mid-canopy trees. Most likely, the physiological response to drought is more conspicuous in young trees or in seedlings/saplings (see e.g. Dawson 1996, Engelbrecht and Kursar 2003) than in adult trees.

During 2002, the third year of the TTEE, the species studied harvested little or no water from depths >2 m in either plot. It is unknown if other life forms are responding in the same way to the treatment, or if the mean depth of water uptake, especially during the dry season, will shift deeper as the soil in the treatment plot gets drier than at present. The setup of the experiment does not allow a complete exclusion of rainfall from the soil,
which is a confounding factor to consider when extrapolating any pattern to possible El Niño drought scenarios. The unexpected results from the January sampling exemplify this confounding effect.

Finally, concurrent measurements of fine root production, stem flow, photosynthetic capacity, water potential, and soil moisture content, among other measurements, should complement a deuterium irrigation experiment. These data should provide a better understanding of the water uptake process at the individual and at the community levels.
LITERATURE CITED


Hodnett M. G., J. Tomasella, Marques Filho, A. de O., and M. D. Oyama. 1996. Deep soil water uptake by forest and pasture in central Amazonia: predictions from long-
term daily rainfall data using a simple water balance model. Pages 79–99
_In: Amazonian Deforestation and Climate (J. H. C. Gash, C. A. Nobre, J. M.
Roberts, and R. L. Victoria, eds.). John Wiley & Sons._

Partitioning of water resources among plants of a lowland tropical forest. _Oecologia_
101: 197–203.

Jackson P. C., F. C. Meinzer, M. Bustamante, G. Goldstein, A. Franco, P. W. Rundel, L.
Caldas, E. Igler, and F. Causin. 1999. Partitioning of soil water among tree species in
a Brazilian cerrado ecosystem. _Tree Physiology_ 19: 717–724.

389–411.

biomass, surface area, and nutrient contents. _Proceedings of the National Academy of
Sciences USA_ 94: 7362–7366.

Belowground consequences of vegetation change and their treatment in models.
_Ecological Applications_ 10: 470–483.

using physiological process in global predictions. _Trends in Plant Science_ 5: 482–
488.

storage and transportation in forests and pastures of seasonally-dry Amazonia.

Plant Physiology. Cambridge University Press.


Leopoldo P. R., W. K. Franken, and N. A. Villa Nova. 1995. Real evapotranspiration and
transpiration through a tropical rain forest in central Amazonia as estimated by the


Table 1. Tag codes and diameter at breast height (DBH) of the trees irrigated in this study. The tag code was assigned by the main investigators of the Throughfall Exclusion Experiment (Nepstad et al. 2002). The DBH was measured in the field at the time of the irrigation.

Trees in the control plot:

<table>
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<th>Species name</th>
<th>January 7 irrigation</th>
<th>May 16 irrigation</th>
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<tbody>
<tr>
<td></td>
<td>Tag code</td>
<td>DBH (cm)</td>
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<tr>
<td>9-35</td>
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<td>9-164</td>
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Trees in the treatment plot:

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<th>DBH (cm)</th>
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Table 2. Numerical values for the van Genuchten (1980) parameters used in the model of soil moisture movement in a clay soil column. The saturated hydraulic conductivity ($K_s$) is the average of the values reported by Tomasella and Hodnett (1996). The values of $n$ and $\alpha$ are the average from two published sources (Rawls et al. 1982 and Carsel and Parrish 1988, summarized by van Genuchten et al. 1991). The values for $\Theta_r$ and $\Theta_s$, expressed here as a volume fraction, are arbitrary but similar to published values. An explanation of each parameter can be found in the Methods section.

<table>
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<tbody>
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<td>$\Theta_r$</td>
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<tr>
<td>$\alpha$ (mm$^{-1}$)</td>
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<td>$n$</td>
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<td>1.2–1.62</td>
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<td>$\ell$</td>
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<td>-</td>
<td>-4.91–5.4</td>
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Table 3. δD average values (± one standard deviation) of the plant samples (n=5 trees per species in each experiment). The depth range at which the deuterium label was above the maximum recorded background δD value in the soil (-12‰) and the depth of the peak deuterium concentration are also shown. Asterisks (*=P<0.05, **=P<0.01) denote significantly higher δD values (one-tailed t test) with respect to background δD values (those from the Pique control plants). The trees in the treatment plot were used for both irrigations while a second set of trees in the control plot was picked for the second irrigation. Depth ranges of above-background δD values and depths of peak deuterium concentrations at each sampling date were calculated using a MATLAB® program.

<table>
<thead>
<tr>
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<th>CONTROL PLOT</th>
<th>TREATMENT PLOT</th>
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<tbody>
<tr>
<td></td>
<td>Coussarea racemosa</td>
<td>Sclerolobium chrysophyllum</td>
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<tr>
<td></td>
<td>(wood cores)</td>
<td>(wood cores)</td>
</tr>
<tr>
<td></td>
<td>207.8 ± 139.3**</td>
<td>39.6 ± 75**</td>
</tr>
<tr>
<td>January 24</td>
<td>-39.1 ± 5.9</td>
<td>-31.2 ± 10.9</td>
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<tr>
<td>(day 17)</td>
<td>-41.2 ± 2.6</td>
<td>-33.9 ± 9.5</td>
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<tr>
<td>May 15/17</td>
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<tr>
<td>June 12</td>
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<tr>
<td>(day 156)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October 15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(day 281)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SECOND IRRIGATION EXPERIMENT (May 16, 2002)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 12</td>
<td>150.0 ± 81.8**</td>
<td>-1.1 ± 23.9*</td>
</tr>
<tr>
<td>(day 27)</td>
<td>-6.2 ± 18.9*</td>
<td>-35.8 ± 8.3</td>
</tr>
<tr>
<td>October 15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(day 152)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Depth range of above-background δD values in the soil.
2 Depth of peak deuterium concentration in the soil.
Table 4. Total amount of water moving up per season at different depths in the soil profile, as calculated by the model of soil water movement in a clay soil column. Total throughfall (mm) at every season is also shown.

<table>
<thead>
<tr>
<th></th>
<th>Total amount of water (mm) moving upwards at different depths</th>
<th>Total throughfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4 m</td>
<td>2 m</td>
</tr>
<tr>
<td>Wet season 2000</td>
<td>4.3</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Dry season 2000</td>
<td>10.1</td>
<td>0.2</td>
</tr>
<tr>
<td>Wet season 2001</td>
<td>5.8</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Dry season 2001</td>
<td>11.6</td>
<td>1.0</td>
</tr>
<tr>
<td>Wet season 2002</td>
<td>1.0</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Dry season 2002</td>
<td>6.9</td>
<td>0.1</td>
</tr>
</tbody>
</table>
**FIGURES**

**Figure 1.** Map of the Floresta Nacional do Tapajós (FNT) showing the Throughfall Exclusion Experiment site (2°53'48.48'' S, 54°57'6.84'' W; Nepstad et al. 2002) with a white star (★). The FNT covers an area of approximately 560,000 ha (Parrotta et al. 1995). Open forests (on upland terrain in the north, but on dissected terrain in the south) are shown in red, while closed forests are shown in green (flat, upland terrain) or yellow (dissected terrain) (map from Parrotta et al. 1995). A Walter climatic diagram (Walter and Lieth 1967) for the city of Santarém is also shown. These diagrams are constructed by plotting both the average monthly total precipitation (mm) and the average monthly temperature (°C) on convenient scales. Precipitation is scaled in 20 mm intervals, while temperature is plotted in 10 °C intervals (2:1 ratio). If monthly precipitation exceeds 100 mm, the precipitation scale is reduced by a factor of 10; the area under this reduced scale is conventionally shaded black to indicate very wet periods. The dotted area indicates the very dry period (drought) when the temperature curve is above the precipitation curve (i.e. when mean monthly precipitation is less than 50 mm). The vertical strips indicate the humid period, when the temperature curve is below the precipitation curve (i.e. when mean monthly precipitation is greater than 50 mm). Data for the Santarém/Taperinha meteorological station (1914–1981) was obtained from www.worldclimate.com.
Figure 2. Graphical representation of the model of soil water movement using four cells as an example. The equations next to each cell describe the movement of water in each cell, and are derived from Darcy’s law (1856) and the Richards equation (1931). The movement of water between cells from time \( t \) to time \( t+1 \) depends on the unsaturated hydraulic conductivity between two contiguous cells \( (K_{i+1/2} \text{ or } K_{i-1/2}) \), the matric potential \( (h) \), the difference in gravitational potential \( (\Delta z) \), and the effect of precipitation \( (P) \) and water uptake \( (U) \). Evaporation \( (E) \) is assumed to be zero. \( K \) and \( h \) depend on the relative water content \( (\Theta) \) of each cell, and on other parameters that describe the physical properties of the soil (see Table 2). The cell height \( (\Delta z) \) used in the model was 200 mm, and the \( \Delta t \) was one hour. Note that the cells have two dimensions (height and width) for graphical purposes only. The actual modeled movement of water is in one dimension only (the vertical \( z \) axis), not in two dimensions.
Figure 3. Graphic representation of the model to determine the mean depth of water uptake ($\mu$), the value used for data analysis. Trees are assumed to harvest water from a linear segment of soil according to a normal distribution. The segment of soil could be located at any depth in the soil profile. I used a standard deviation ($\sigma$) equal to 8.33 cm, which means that 99.7% of the water being taken up is assumed to come from a vertical segment of soil 50 cm long (ca. $\mu \pm 3\sigma$).
Figure 4. Percolation of deuterated water in the first irrigation experiment. Trees were irrigated at the beginning of the wet season, on January 7, 2002. The treatment plot was covered with panels from January 1 to July 1. Note the scale differences of the $\delta^D$ axis as the deuterium concentration in the soil diminishes over time. Error bars represent ± one standard error of the mean. Depths of peak deuterium concentrations at each sampling date were calculated using a cubic spline interpolation program in MATLAB®. This interpolation was graphed as a curve using SigmaPlot®.
Figure 5. Upward movement of the deuterium label from the first irrigation during the 2002 dry season in the control plot. The dotted line represents the June 12 sampling (day 156; n=4 soil cores) and the continuous line the October 15 sampling (day 281; n=2 soil cores). Error bars represent ± one standard error of the mean. Depths of peak deuterium concentrations at each sampling date were calculated using a cubic spline interpolation program in MATLAB®. This interpolation was graphed as a curve using SigmaPlot®.
Figure 6. Percolation of deuterated water in the second irrigation experiment. Trees were irrigated at the end of the wet season, on May 16, 2002. Panels in the treatment plot were removed on July 1, 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. Error bars represent ± one standard error of the mean. Depths of peak deuterium concentrations at each sampling date were calculated using a cubic spline interpolation program in MATLAB®. This interpolation was graphed as a curve using SigmaPlot®.
**Figure 7.** Relationship between depth of deuterium peak in the soil profile and cumulative amount of throughfall reaching the soil when (1) it is not covered by panels (i.e. data from the control plot all year long, the treatment plot during the dry season, and the site next to the plots reported by Sternberg et al. 2002), and (2) when it is covered by panels (i.e. data from the treatment plot during the wet season). Circles represent sampling dates of the first irrigation: the treatment plot (○) and the control plot (●) were sampled on January 9, 15, 24 and May 15. The June 12 and October 15 samplings in the control plot were excluded from this analysis because they show the deuterium peak moving upwards. Squares represent sampling dates of the second irrigation: the treatment plot (□) and the control plot (■) were sampled on May 22, June 12 and October 15. The May 22 and June 12 data from the treatment plot were analyzed as if the panels already had been removed, although they were actually removed on July 1, 2002 (see Methods for further explanation). Triangles (▲) represent the deuterium peak depths in the Sternberg et al. (2002) study.
Figure 8. Amount of water per day moving upwards at different depths (1 m, 2 m and 4 m) in a clay soil column, as predicted by the model of soil moisture movement (Figure 2). The top graph shows the actual throughfall measurements that served as input for the model. Other input included initial water content measurements (taken from field measurements) and various parameters describing the physical properties of clay soils (see Table 2). The model was run independently for each season (assuming that the wet season and the dry season began on January 1 and July 1, respectively). Note the differences in scale on the y-axis.
Figure 9. Mean depths ($\mu$) from which *Coussarea racemosa*, *Sclerolobium chrysophyllum*, and *Eschweilera pedicellata* are taking up water, as inferred from the deuterium signatures of the plants (Table 3) and the deuterium profiles of the soil (Figures 4 and 6). The mean depths were calculated using a model that assumes trees take up water according to a normal distribution of $\sigma = 8.33$ cm (Figure 3). The number below each column is the sample size, i.e. the number of trees (out of five in each species) that had a solution in the model. The probabilities of a two-tailed t test performed between control and treatment plots are also shown. Error bars represent $\pm$ one standard deviation.
Figure 10. Expected profiles of deuterium abundance in the soil as a consequence of hydraulic lift, and possible root distributions explaining the process. Full functionality of all roots shown is assumed. The y-axis scale represents the approximate depths at which upward movement of water was observed in this study (from ~2.5 m to ~2 m; Figures 4 and 5). In the left root profile, water is absorbed at 2.5 m and deposited at 2 m overnight; as a result, two δD peaks should be observed. This is the classic model of hydraulic lift, except that plants may instead deposit the absorbed water near the surface. In the right root profile, water is absorbed 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. The original deuterium profiles are indicated by a dotted line which overlaps the expected deuterium profile.
APPENDICES

Appendix 1. Model of soil water movement

The simulation model was written in MATLAB® and contains commands (in bold) and comments (preceded by “%”). The comments have been minimized; please refer to the Methods section for further details. When entering data, be consistent with units (length and time). I used mm and hour in this study, but units could be different if desired. TDR values (volumetric water content, i.e. fractions) should be transformed to units of length. Because of limitations inherent in the model, it is better to use a short Δt and a large Δz, as well as a low Θ_r and a high Θ_s. The short program designed to calculate the amount of water moving up at a given depth is also appended.

%******** DATA INPUT ********

clear all;
display('Be consistent with the units. Use the same length and time units for *all* input.');
%defining cell size (cell)
maxdepth=input('\nWhat is the maximum depth of the soil profile (a multiple of 10)?\n');
%e.g. 5000 mm
cells=input('\nHow many cells do you want?\n'); %e.g. 25 for a 200 mm cell
cell=maxdepth/cells; %gives the cell height (e.g. 200 mm)
deltaz=cell %delta z is equal to cell height

%creating the fine cell vector (Fincells); cells are indexed, starting with number 1
Fincells=linspace(1,maxdepth,cells)';
if cell>1
    Fincells=linspace(0,maxdepth,cells+1)';
    Fincells(1)=1 %displays the Fincells vector; if incorrect, quit by pressing Ctrl-C
end

% subroutine to define root distribution (R) if cell=1
R=zeros(length(Fincells),1);
R(1)=(1-(.962^Fincells(1)))-(1-(.962^0));
for d=2:length(Fincells)
    R(d)=(1-(.962^Fincells(d)))-(1-(.962^Fincells(d-1)));
end

% subroutine to define root distribution (R) if cell>1
if cell>1
    R=zeros(length(Fincells),1);
    R(1)=(1-(.962^Fincells(2)))-(1-(.962^0));
    for d=2:length(Fincells)-1
        R(d)=(1-(.962^Fincells(d+1)))-(1-(.962^Fincells(d)));
    end
    R(end)=(1-(.962^(Fincells(end)+cell)))-(1-(.962^Fincells(end)));
end
% defining initial water content conditions and soil parameters
TDRcells=input('Enter the cells at which TDR measurements ("TDRcells") were made, starting with [1...]
');
% e.g. [1 300 500 1000 2000 3000 4000 5000], these are the cell's indexes

TDRtime1=input('Enter the initial volumetric water content measurements for each TDRcell in the same units as the water content');
% e.g. [88 88 78 62 60 58 58 56] mm if cell size=200 mm (e.g. TDR value = 88/200 = 0.44)

maxsat=input('Enter the saturated water content for each TDRcell in the same units as the water content');
% e.g. [120 120 120 120 120 120 120 120] mm if maximum saturation is TDR=0.6 and cell=200 mm

minsat=input('Enter the residual water content for each TDRcell in the same units as the water content');
% e.g. [20 20 20 20 20 20 20 20] in mm if minimum saturation is TDR=0.1 and cell=200 mm

deltat=input('Enter the delta t in units of time');
% e.g. [1] hour, delta t=1 time interval usually

Ksat=input('Enter the saturated hydraulic conductivity (length/time units) for each TDRcell in the same units as delta z and delta t');
% e.g. [550 550 550 550 550 550 550 550] mm/hour

alfa=input('Enter "alfa" van Genuchten parameter for each TDRcell (1/length units) in the same units as delta z');
% e.g. [.00175 .00175 .00175 .00175 .00175 .00175 .00175 .00175] in 1/mm

n=input('Enter "n" van Genuchten parameter for each TDRcell');
% e.g. [1.11 1.11 1.11 1.11 1.11 1.11 1.11 1.11] no units

L=input('Enter "l" parameter of Van Genuchten equation for each TDRcell');
% e.g. [.5 .5 .5 .5 .5 .5 .5 .5] no units

% interpolating soil parameters for every cell ("Fine" vectors) using a cubic interpolation
for d=1:length(Fincells)
    FinTDRtime1(d,1)=interp1(TDRcells,TDRtime1,Fincells(d),'cubic');
    Finmaxsat(d,1)=interp1(TDRcells,maxsat,Fincells(d),'cubic');
    Finminsat(d,1)=interp1(TDRcells,minsat,Fincells(d),'cubic');
    Fin_n(d,1)=interp1(TDRcells,n,Fincells(d),'cubic');
    Finalfa(d,1)=interp1(TDRcells,alfa,Fincells(d),'cubic');
    FinL(d,1)=interp1(TDRcells,L,Fincells(d),'cubic');
    FinKsat(d,1)=interp1(TDRcells,Ksat,Fincells(d),'cubic');
end
% entering the precipitation (Pinput) and transpiration (Tinput) data
YN=input('
Do you want to transform the throughfall and transpiration from [length]/day to [length]/hour? (if not, just press enter) Y/N [N]: ','s');
% if you don't, just press enter
if isempty(YN)
    YN='N';
    Pinput=input('Enter throughfall vector in [length/time]
use the same units as delta z and delta t
')';
    % e.g. [.3 .2 .4 .1 0 .2 0] mm/hour, for seven hours
    Tinput=input('Enter transpiration vector in [length/time]
use the same units as delta z and delta t
')';
    % e.g. [.17 .17 .17 .17 .17 .17 .17] mm/hour, assuming constant transpiration during seven hours
else
    pday=input('Enter throughfall vector in [length/day]
these values will be transformed to [length]/hour
and the appropriate Pinput vector created
')';
    % e.g. [4 5 0 0 2 10 4] mm/day, for seven days
    tday=input('Enter transpiration vector in [length/day]
these values will be transformed to [length]/hour
and the appropriate Tinput vector created
')';
    % e.g. [4 4 4 4 4 4 4] mm/day, for seven days
    ptemp=zeros(24,length(pday));
    ttemp=zeros(24,length(tday));
    for c=1:length(pday) % each column "c" represents one day
        for r=1:24 % from 0 am to 12 pm (all day long)
            ptemp(r,c)=pday(c)/24;
            % gives throughfall values in mm/hour for each day
        end
        for r=7:18 % from 6 am to 6 pm (12 hours of transpiration)
            ttemp(r,c)=tday(c)/12;
            % gives transpiration values in mm/hour for each 12-hour daylight interval
        end
    end
    % creating throughfall and transpiration column vector in mm/hour
    Pinput=reshape(ptemp,(24*length(pday)),1); % throughfall vector
    Tinput=reshape(ttemp,(24*length(tday)),1); % transpiration vector
end
% ******** MATRIX/VECTOR DEFINITION ********
% Here I define the matrices in which the model outputs at each time interval will be saved. These matrices are not strictly necessary to run the model, but if created beforehand and filled with zeros, they speed up the simulation.

water=zeros(length(Fincells),length(Pinput)+1); water(:,1)=FinTDRtime1;
% water content matrix

Pav=zeros(length(Fincells),length(Pinput));
% available precipitation to be contributed to a given cell

A=zeros(length(Fincells),length(Pinput));
% water content available in each cell before it saturates

P=zeros(length(Fincells),length(Pinput));
% actual amount of precipitation that is contributed to each cell

U=zeros(length(Fincells),length(Pinput));
% water uptake matrix

Se=zeros(length(Fincells),length(Pinput));
% effective saturation matrix

h=zeros(length(Fincells),length(Pinput));
% matric potential matrix

h2=zeros(length(Fincells),length(Pinput));
% matric potential matrix divided by delta z and transformed to negative values

atemp=zeros(length(Fincells),length(Pinput));
% "a" part of the Kunsat formula

btemp=zeros(length(Fincells),length(Pinput));
% "b" part of the Kunsat formula

Kunnum=zeros(length(Fincells),length(Pinput));
% numerator of the Kunsat formula

Kunsdenom=zeros(length(Fincells),length(Pinput));
% denominator of the Kunsat formula

Kunsat=zeros(length(Fincells),length(Pinput));
% unsaturated hydraulic conductivity matrix

Kav=zeros(length(Fincells),length(Pinput));
% average unsaturated hydraulic conductivity matrix
%******** RUNNING THE BIG LOOP ********

for t=1:length(Pinput) %Number of times (t) the loop will run

%THROUGHFALL EFFECT
if Pinput(t)>0
    A(:,t)=Finmaxsat-water(:,t); %calculates how much water each cell can accept (how much is "available")
    Pav(1,t)=Pinput(t); %amount of precipitation falling on the first cell at time t
    for d=1:length(Fincells)
        if Pav(d,t)>A(d,t)
            P(d,t)=A(d,t); %contribution of the precipitation to the cell; cell becomes saturated
            Pav(d+1,t)=Pav(d,t)-A(d,t); %amount of precipitation that is left and filtrates to the next cell
        else
            P(d,t)=Pav(d,t); %contribution of the precipitation to the cell, since it is less than the amount the cell can support (A),
            Pav(d+1,t)=0; %because there would be no more precipitation left.
        end
    end
end

%WATER UPTAKE, HYDRAULIC CONDUCTIVITY, MATRIC POTENTIAL
%AND GRAVITATIONAL POTENTIAL EFFECTS
if sum(Ksat)>0 %effective saturation vector (Se); it has no units
    Se(:,t)=(water(:,t)-Finminsat)./(Finmaxsat-Finminsat);
    if Tinput(t)>0
        U(:,t)=(R.*Se(:,t)).*Tinput(t); %U=T only if Se=1
    end
end

%soil matric potential (h) in units of length (pressure heads)
    h(:,t)=([(Se(:,t).*(Fin_n./((1-Fin_n)))-1).^((1./Fin_n))]./Finalfa;

%unsaturated hydraulic conductivity (Kunsat)
    atemp(:,t)=(Finalfa.*h(:,t)).^((Fin_n-1)); %part "a" of the formula
    btemp(:,t)=1+((Finalfa.*h(:,t)).^((Fin_n))); %part "b" of the formula
    Kunsnum(:,t)=FinKsat.*[1-[atemp(:,t).*btemp(:,t).^((1-Fin_n)./Fin_n)].^2];
    Kunsdenom(:,t)=btemp(:,t).^[((Fin_n-1)./Fin_n).*FinL];
    Kunsat(:,t)=Kunsnum(:,t)./Kunsdenom(:,t);

%Kunsat calculated above is for each cell;
%to calculate the water content, the average conductivity (Kav)
%between two adjacent cells should be used.
%Kav is the K(i+1/2) or K(i-1/2) in equation 2.
for d=1:length(Fincells)-1
    Kav(d,t)=(Kunsat(d,t)+Kunsat(d+1,t))/2;
end

%building the unsaturated hydraulic conductivity matrix (Hydcond)
Hydcond=zeros(length(Fincells),length(Fincells));
Hydcond(1,1)=-Kav(1,t);
Hydcond(1,2)=+Kav(1,t);
for d=2:length(Fincells)-1
    Hydcond(d,d-1)=+Kav(d-1,t);
    Hydcond(d,d)=(-Kav(d-1,t)-Kav(d,t));
    Hydcond(d,d+1)=+Kav(d,t);
end
Hydcond(d+1,d)=+Kav(d,t);
%creating the first missing value in the last row of the matrix
Hydcond(end,end)=-Kav(d,t);
%creating the second missing value in the last row of the matrix

%building the unsaturated hydraulic conductivity vector (Hydcond2)
Hydcond2=zeros(length(Fincells),1);
Hydcond2(1)=-Kav(1,t);
for d=2:length(Fincells)-1
    Hydcond2(d)=(+Kav(d-1,t)-Kav(d,t));
end
Hydcond2(end)=+Kav(d,t); %creating the last element of this vector

%WATER CONTENT CALCULATION (MATRIX/VECTOR EQUATION)
%To calculate the new water content at time t+1,
%the matric potential (h) vector will be transformed to negative values
%and divided by delta z (deltaz) to create the h2 vector.
%The h2 vector will be multiplied by the Hydcond vector,
%and the Hydcond2 vector added.
%The h vector needs to remain positive to calculate Kunsat.

h2(:,t)=-h(:,t)./deltaz;
water(:,t+1)=water(:,t)+P(:,t)-U(:,t)+delta t*[Hydcond*h2(:,t))+Hydcond2];
%evaporation is not included in this equation because it is assumed to be zero
end
end

%%%%%% end of program %%%%%%
Program to calculate the amount of water moving up at a given depth

%We are interested to know how much water moved up at a given depth;
%let’s call this depth the ”threshold depth”.
%The threshold depth (a cell) must be input as an index (a number) of the Fincells vector.
%To correctly select such threshold depth index, one must check:
% 1. The Kav between the cell at the threshold depth and the cell below it.
%  Kav is the unsaturated hydraulic conductivity between two consecutive cells.
%    e.g. if threshold depth=100 cm and cell size=1 cm, then the program should use
%      the Kav between cell index 101 (101 cm) and cell index 100 (100 cm).
%    e.g. if threshold depth=100 cm and cell size=20 cm, then the program should use
%      the Kav between cell index 7 (120 cm) and cell index 5 (80 cm).
% 2. The h2 between the cell at the threshold depth and the cell below it.
%  h2 is the matric potential, already negative and divided by delta z.
%
%Because this program uses the ”pday” variable from the program of soil moisture movement,
%it only works for [length]/hour units. It can however be easily modified for other units.

clear i; clear up; clear upday; clear sumup; clear down; clear downday; clear sumdown;
i=input('Enter the index of the threshold depth (see Fincells vector)  ');
up=zeros(1,length(Pinput)); %Pinput needs to be in [length]/hour
down=zeros(1,length(Pinput));
for t=1:length(Pinput)
    if [(h2(i+1,t)-h2(i,t))-1]>0
        up(t)=Kav(i,t)*[(h2(i+1,t)-h2(i,t))-1];
    else
        down(t)=Kav(i,t)*[(h2(i+1,t)-h2(i,t))-1]; %if [(h2(i+1,t)-h2(i,t))-1)]<=0
    end
end

%%%Calculating the amount of water moving up from below to above the threshold depth%%% 
upday=reshape(up,24,length(pday)); %from hours to days; each column in ”upday” matrix represents one day
sumup=sum(upday)';
%each row in the ”sumup” vector represents the total amount of water moving up at each day
%these were the values graphed in Figure 8.

%%%Calculating the amount of water moving down from above to below the threshold depth%%% 
downday=reshape(down,24,length(pday));
sumdown=sum(downday)';

%%%%%% end of program %%%%%%
Appendix 2. Model to determine mean depth of water uptake by plants

The model was written in MATLAB® and contains commands (in bold) and comments (preceded by “%”). The ‘Normal’ function program, also written in MATLAB®, is shown at the end. Comments have been minimized; please refer to the Methods section for further details. The program coding was originally written by Dr. Leonel Sternberg.

%******** DATA INPUT ********
Depth=input('Enter the depth of measurements vector\n');
% e.g. [1 20 40 60] cm, each number actually represents a cubic unit of soil

Soil=input('Enter average isotopic composition of soil water at each depth\n');
% e.g. [13 196 36 -13] in delta D units

Plant=input('Enter isotopic composition of each plant to be analyzed\n');
% e.g. [23 94 10 93 196] in delta D units; this is the observed isotopic composition

%generating the fine depth vector
FinDepth=linspace(1,max(Depth),max(Depth));
%vector starts at "one" instead of zero, because the isotopic composition
%is obtained from volumetric units of soil

%interpolating the soil isotopic ratio for each 1 cm depth interval
for d=1:length(FinDepth)
    FinSoil(1,d) = interp1(Depth,Soil,d,'*cubic');
end

%******** CALCULATIONS ********

global SDEV;
SDEV=input('Enter standard deviation of the soil segment for plant water uptake\n');
% e.g. [8.33] if plants are assumed to harvest water from a 50 cm segment of soil

for p=1:length(Plant)
    for k=1:max(FinDepth) %k=1 because the first cell is 1, the first volume unit of soil
        global deep;
        deep=k;
        %Normal Equation
        Perc=Normal(FinDepth);
        %area under curve
        area=quadL('Normal',1,max(Depth));
        %correcting proportions of water uptake so that they add up to one (or almost one)
        cPerc=Perc*(1/area);
        %cross product of proportions with isotope ratios of soil water vector;
        %this is the calculated isotopic composition (in delta D units)
        Isoplant=sum(cPerc.*FinSoil);
    end
end
%comparing the calculated isotopic composition to the observed isotopic composition
Delta(k)=Isoplant-Plant(p);
end

%calculating all possible mean depths (Dpt) of water uptake
i=1;c=1;
for m=1:length(Delta)-1
%it is "length(Delta)-1" because of the "m+1" expressions in the loop
if Delta(m)>0
  if Delta(m+1)<0
    slp=(Delta(m+1)-Delta(m))/(FinDepth(m+1)-FinDepth(m));
    Dpt(p,c)=((FinDepth(m+1)*slp)-Delta(m+1))/slp;
    i=i+1;c=c+1;
  end
elseif Delta(m)<0
  if Delta(m+1)>0
    slp=(Delta(m+1)-Delta(m))/(FinDepth(m+1)-FinDepth(m));
    Dpt(p,c)=((FinDepth(m+1)*slp)-Delta(m+1))/slp;
    i=i+1;c=c+1;
  end
else
    Dpt(p,c)=FinDepth(m); %if Delta(m)=0, an infinitesimal possibility
    i=i+1;c=c+1;
  end
end
if i==1 %if Delta(m) never crosses the zero threshold...
  Dpt(p,c)=-1; %the "-1" represents an unsolvable solution
  c=c+1;
end
clear Delta
end
Dpt(:,end+1)=Plant' %displaying final output
%Each row shows all possible mean depths of water uptake for a given plant;
%the observed isotopic composition of each plant analyzed
%is shown in the rightmost column.
%%%%%% end of program %%%%%%

'Normal.m' function file
%This is the 'Normal.m' file that should be saved
%in the same directory as the depth of water uptake model.
function P=Normal(B)
global deep; global SDEV
Pow=(((B-deep)*(1/SDEV)).^2)*(-0.5);
P=(1/(SDEV*2.50663))*(exp(Pow)); %%%%% end of program %%%%%%
Appendix 3. Documentation CD

The accompanying CD contains a PDF file of the thesis, an Excel file with the soil and plant data (master file), and a Powerpoint slide-show of the defense (September 12, 2003) which includes pictures of the study area.
VITA

Hugo Geovanny Romero-Saltos was born in Quito, Ecuador, on January 30, 1974. His parents are Hugo B. Romero and Dora B. Saltos. In October 1992 he entered the Department of Biological Sciences of the “Pontificia Universidad Católica del Ecuador” (PUCE) where he graduated as a “Licenciado en Ciencias Biológicas” (B.S. in Biology) in March 1999. His B.S. thesis was entitled "Diversidad, análisis estructural y aspectos florísticos relevantes de las lianas en una parcela de bosque muy húmedo premontano, Amazonía Ecuatoriana". From 1998 to 2000, he worked at the Herbarium QCA (PUCE) with an international collaborative project to assess the potential for sustainable extraction of non-timber plant products in northwestern Amazonia, and with a project that compiled biological information relevant to the conservation of the endemic Ecuadorian flora. He co-authored chapters or sections of two books that resulted from these projects: “Libro Rojo de las Plantas Endémicas del Ecuador” (2000) and “Evaluación de recursos vegetales no maderables en la Amazonía noroccidental” (2001). In August 2000, he began his graduate studies in the Department of Biology at the University of Miami with a Fulbright/LASPAU scholarship. He was granted the degree of Master of Science in December 2003.

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