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Vertical patterns of soil water uptake by plants in a primary forest and an abandoned pasture in the eastern Amazon: an isotopic approach

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Abstract

This study evaluated the water uptake patterns of a primary forest and of the savanna-like vegetation of an abandoned pasture in an eastern Amazon site. We used natural stable isotope abundance in the soil profile, as well as plots irrigated with deuterated water to determine time and depth of soil water uptake by plants in different functional groups. Natural isotopic abundance was not suitable for identification of depth of water uptake by plants, but experiments using labeled water were. We found that the label percolation rate in the soil profile of the forest was lower than that observed in the pasture. Fourteen months after application, the label peak was located at 1.8 m depth in the forest and at 3 m depth in the pasture. Isotopic analysis of sap water from trees and lianas in the forest during the dry season showed that trees acquired labeled water at a deeper level in the soil profile compared to that acquired by lianas. Depth of water uptake by lianas seems to vary on a seasonal basis. In the pasture the 'colonizer' shrub (*Solanum crinitum* Lamb.) took up labeled water only from the surface layer of the soil profile ($\sim$20%), whereas the most abundant coexisting grass (*Panicum maximum* Jacq.) acquired it from the top meter. None of the pasture plants were able to acquire labeled water after one rainy season when the label pulse was deep in the soil ($>$1 m deep). These results have implications for studies of forest water cycle in which the soil volume used as source of water for plant transpiration is still unknown, and for an understanding of plant succession in the forest regeneration process of abandoned pastures in the eastern Amazon.

Introduction

In studies of the soil-plant-atmosphere continuum, the soil compartment is the least understood because of inherent difficulties in observing underground processes. Any inference of plant root distribution without excavation is suspect because of influences of the chemical and structural properties of soil, plant health conditions and the inherent root/shoot characteristics of species. Even when using excavations, root identification and measurement are tedious and time-consuming. Furthermore, the presence of root in the soil profile alone does not necessarily imply root water uptake (Ehleringer and Dawson, 1992). Root distribution and function studies, however, are important in explaining the distribution of vegetation worldwide. For example, the Walter equilibrium model (Walter, 1979) suggests that grass and woody vegetation in savannas co-exist because of spatial and temporal soil water resource partitioning (Le Roux et al., 1995; Scholes and Walker, 1993; Schulze et al., 1996; Walker and Langridge, 1997; Weltzin and McPherson, 1997). Even where water does not seem to be a limiting factor, different strategies of nutrient uptake are necessary to allow great species variety coexistence. It is long believed that roots in Amazon forests occupy only the topsoil layers ($<$1 m depth); in fact, ecosystem and General Circulation Models (GCM) assume shallow rooting depth (Nobre et al., 1991; Potter et al., 1993; Shukla et al., 1990). This dogma may confound plant

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water uptake interpretation. However, there is new evidence that deeper soil layers are important in the maintenance of evapotranspiration during dry periods (Hodnett et al., 1995; Jipp et al., 1998; Moreira et al., 1997; Nepstad et al., 1994). We are still missing direct evidence of soil water uptake at depth. We also do not know how different types of plant species vary in their ability to tap deep soil moisture (Jackson et al., 1995). This paper employs stable isotopes to test the hypothesis that plants are tapping deep soil layers, and to examine difference in vertical patterns of soil water uptake between different types of plants.

The latest technological tool in below-ground studies is the use of stable isotopes. The isotopic technique may be used to infer root distributions. Measurement of the stable isotopes allows identification of roots from different plant groups based on the difference of the carbon isotopic content of groups with distinct photosynthetic characteristics, mainly C_3 and C_4 plants (Le Roux et al., 1995; Sternberg at al., 1998; Svejcar and Boutton, 1985). Many grasses are C_4 plants with a high content of ^{13}C, while most of the shrubs and trees in the primary forest are C_3 plants. The proportion between roots of these major plant groups in the soil profile for sites ranging from pasture to forest (or vice versa) may be then studied by carbon stable isotopic analysis (e.g. Scholes and Walker, 1993).

Stable isotopes have also been used to aid studies on soil resource exploitation by plants. This type of work is based on the presumed difference in ^{18}O and ^{2}H (also known as deuterium, D) of the soil water along the soil profile due to natural enrichment of the surface water by evaporation. Natural differences in the soil profile and between soil and ground water (e.g. Dawson and Ehleringer, 1991; Ehleringer et al., 1991; Ewe et al., 1999; Hodnett et al., 1995; Ish-Shalom-Gordon et al., 1992; Jackson et al., 1995; Le Roux et al., 1995; Schulze et al., 1996; Sternberg and Swart, 1987; Weltzin and McPherson, 1997), as well as studies using labeled water (e.g. Araguás-Araguás et al., 1995; Caldwell and Richards, 1989; Förstel et al., 1991; Lin et al., 1996; Planboeck et al., 1999; Walker and Richardson, 1991) can be used to indicate depth of plant water acquisition. The technique has the advantage of working with plant water without significant disturbance of the plant root system in which, for example, the biological interaction between roots and fungi (mycorrhizae) may substantially increase soil resource utilization by the plant (Janos, 1987, 1996).

In this study, we used isotope techniques to establish water uptake patterns in an eastern Amazon site. In spite of a pronounced dry season, plants in the eastern Amazon forests are a potential water vapor feeder to the Amazonian atmosphere as they remain evergreen and continue to transpire (Dall'Olio et al., 1979; Gat and Matsui, 1991; Salati et al., 1979; Victoria et al., 1991). An understanding of deep soil water utilization can have implications for forest management policies and for applied hydrology of the Amazonian ecosystem.

We used natural stable isotope abundance in the soil profile, as well as plots irrigated with deuterated water to test hypotheses concerning water uptake by different plant functional groups in a primary forest and in an abandoned pasture. Furthermore, we tested the effect of these vegetation types on the percolation rate of water through the soil profile. Specifically, we tested whether or not:

(a) Forest plants could access water at depth below 1 m in the soil profile;
(b) Individuals of a small colonizer tree (*Solanum crinitum* Lamb.) in an abandoned pasture were able to access water at deeper layers of the soil profile than the grasses (*Panicum maximum* Jacq.), and;
(c) The percolation rate of water in an abandoned pasture differed from that in a primary forest.

Materials and methods

Site

Experiments were conducted in the eastern Amazon (Brazil) where different types of vegetation and land use are present. The site was at the Vitoria farm located near the town of Paragominas (3° S, 47° W) in the state of Pará. At Vitoria farm, pastures of different ages and degradation levels surround patches of primary forest (Nepstad et al., 1991, 1994). In the pastures, the flat landscape is dominated by *Panicum maximum* Jacq., but punctuated with treelets (*Solanum crinitum* Lamb.) and shrubs (e.g. *Guatteria poepigiana* Mart., *Rolandra argentea* Rottbn.) referred to here as colonizing species. Some of the older abandoned pastures have regrown to the secondary open forest structure known as *capoeira*. At this site, we took advantage of the proximity of degraded pastures to a 250 ha primary forest patch. Dry conditions prevail during the June–December summer season. Fifteen percent of

the average annual rainfall (1800 mm) occurs during the dry season. In spite of the long water shortage, forest patches remain evergreen while pastures usually exhibit signs of 'dormancy' during the dry season (Nepstad et al., 1994).

The above-ground forest biomass averages 300 t/ha (Carvalheiro and Nepstad, 1996; Nepstad, 1989) and the canopy height may reach 40 m in undisturbed lots. Primary and secondary forests in the almost flat landscape show a leaf area index (LAI) of 5–5.5, and a small reduction of this index during the dry season (Nepstad et al., 1994; Restom, 1996).

Soils are kaolinitic red-yellow Latosols (Haplustox), deeply weathered and well drained, with a very low water table (deeper than 45 m, Nepstad et al., 1991, 1994, 1996).

Natural stable isotope abundance measurements

Soil samples collection

Natural stable isotope abundance in the soil water from primary forest and pasture was first evaluated in three core replicates of the soil profile, which were gathered on November 4–6th, 1994. About 30–40 g of soil were sealed in screw-cap culture tubes with Parafilm and were kept frozen until water distillation in vacuum line. Samples were collected from the surface (0–5 cm), 0.5, 1, 2, 4 and 6 m depth in the forest and down to 4 m in the pasture.

Plant collection

Well suberized stems (10 cm long and up to 1 cm in diameter) were collected from trees (Dawson and Ehleringer, 1993). For grass samples, thick fleshy culms covered with dry leaves to minimize the effect of transpirational enrichment were harvested. Among the plant species collected in the forest were two lianas (*Bauhinia* sp. and *Memora* sp.) and the tree species *Lecythis idatimon* Aubl. (Jatereu), *Diospyros duckei* Sandw (Kaki Preto), *Rinorea guianensis* Aublet (Guariquarana), in addition to one known by the common name of Tacacazeira. Three stem replicates (different individuals) of each of the six species in the forest and five replications of the *S. crinitum* stems and *P. maximum* culms in the pasture were collected during the same 3 days as the soil samples.

Deuterated water pulse-chase experiment

Plot description

Square plots (2 × 2 m) in the forest were chosen to have the largest number of physiognomic plant groups possible. We found individuals of several ages and life stages (average 17 individuals/plot). Saplings were identified only by common name. Species replication was rare because the forest understory is very heterogeneous and the plots were small. Plots (2 × 2 m) in the abandoned pasture were covered with 1.2–1.5 m tall grass (*P. maximum*) and they contained at least one treelike *S. crinitum* and in one case a *G. poepigiana* shrub.

For the pulse-chase experiment, two treatment plots were labeled with deuterated water by surface irrigation in each area. Plant samples and soil cores from nearby areas more than 10 m away from irrigated plots were taken during each collection as control samples. In the forest plots, surface litter was carefully removed before deuterated water (3 l) was sprinkled over the soil surface, and then the leaves were spread evenly back on the plots. All plants above the seedling stage inside the forest plots were tagged.

Label preparation and irrigation

Label for irrigation was prepared as in Araguás-Araguás et al. (1995). Deuterated water (250 mL of 99.8% D_2O) was dissolved in 12 l of local water with an average isotopic composition (or δD, read delta D) of −22‰ (SMOW). Delta notation is used to express small natural variations in the isotopic composition of compounds, and it measures the deviation of a sample's isotopic ratio to that of an international standard for a particular isotope. Because the numbers are very small, delta value is multiplied by 1000 to express the deviation per mil (‰). Mathematically, δD (per mil) of a water sample relative to SMOW (Standard Mean Ocean Water) is given by δD (‰) = $[(R_{\text{water}}/ R_{\text{SMOW}}) - 1] \times 1000$, where R represents the molar ratio of the 'heavy' isotope (deuterium) to the most common 'light' isotope, hydrogen. The initial δD value of the label was about +130 000‰. Three liters of this deuterium-enriched solution were spread evenly on each plot using a watering can. An additional 2.5 l of natural water were irrigated in each plot (bringing the δD of applied water to a value of $\sim$ +71 300‰) in order to push the label downwards and to avoid loss of label by excessive evaporation. This volume, equivalent to ∼1.4 mm of rainfall, is insignificant compared to the annual rainfall of about 1800 mm. Plots were irrigated on April 19th, after three fourths of the 1996 rainy season (about 1600 mm) precipitation had occurred. This procedure allowed the soil profile to be recharged to the point that

labeled water could percolate freely downward pushed by subsequent rain events as in a piston flow (Förstel et al., 1991). Rainfall was monitored from the initiation to the end of the experiment.

Collections of plant and soil samples were made on April 22nd, July 8–11th and December 11–16th, 1996 and once again on June 1st, 1997. The first collection was made during the rainy season, 3 days after label irrigation. The second and third collections were made during the 1996 dry season, approximately 3 and 8 months after irrigation, and a final collection after the 1997 rainy season was made 14 months after label irrigation.

Soil sample collection

An isotopic soil water profile was established by analysis of water extracted from soil samples at different depths in the soil profile (every 0.2 or 0.5 m). For every collection, two replicate cores from each plot were obtained in addition to two control cores. In each core, 30–40 g samples were manually removed every 0.2 m (or 0.5 m) down to 6 m deep using a 4" manual auger. Samples were stored in Parafilm sealed culture tubes and frozen until water extraction by vacuum distillation. Three months after irrigation, a core was also taken 0.5 m outside the plots to determine horizontal movement of water and the associated deuterium label.

Labeled soil data treatment

Average soil profile enrichment values were calculated for each environment (forest and pasture) by subtracting control isotopic values from the average for the treated core values. Label concentration changes over time were evaluated by taking the integral of the graph area, showing the isotope enrichment of the soil profiles in treated plots relative to control plots.

Plant samples

The following species were collected in the forest treatment plots: *Eugenia biflora* DC (Murta, 2 trees), *Memora flavida* (DC) Bur. & K. Schum. (Cipó Vermelho, 1 liana), *Bauhinia guianensis* (Escada de Jaboti, 4 lianas), *Poecilanthe effusa* Benth. (Gema de ovo, 2 trees), *Cassia ensiformis* Vell. (Coração de negro, 1 tree), *Newtonia suaveolens* (Miq) Breaun (Timborana, 1 tree), *Memora* sp. (6 lianas), *Pithecolobium* sp. (Ingarana, 1 tree), *Oenocarpus bacaba* (Bacabeira, 1 tree), *Parkia* sp. (Faveira, 1 tree) and other undetermined species known as Arataciú (Euphorbiaceae, 2 trees), Caniço Preto (3 trees), Indiraborana (1 tree), Abiu (2 trees), Taboca (1 liana), Iperana (1 tree), Abiu Amarelo (1 tree), Espeteira (1 tree) and Espinheira (1 tree).

We used well suberized plant stems as in prior samples. We did not collect control plants for pasture or control lianas in the forest 3 days after irrigation; we collected only control trees. For the first collection of nearby control plants, we used six unknown tree species, two individuals of *Parkia* sp. (Faveira), a *Cecropia* sp. (tree) and a *Newtonia suaveolens* (Miq) Breaun (Timborana, tree). For the second collection of plant control samples, in addition to those 10 samples we also collected a *Memora* sp., a *Bauhinia* sp., and another liana known as Taboca. Because we suspected possible contamination of some individuals, the final two collections of control plants were made at a considerable distance from the treated plots. In these samplings, we collected a *Diospyros duckei* Sandw (Kaki Preto, tree), a *Heteropsis* aff. *spruceana* Schott (Cipó Titica, liana), a *Bauhinia* sp., a *Memora* sp., an Euphorbiaceae known as Arataciu (tree), two lianas known as Cipó Espinho and Cipó Branco and other trees known by the common name of Quariquarana, Abiu da folha grossa and Iperana. All plant samples were sealed in culture tubes as previously done and taken to the laboratory for water distillation and isotopic analysis.

Plant data treatment in the label experiment

In order to estimate the quantity of water uptake by plants at the particular depth of the soil where the deuterium label was present, we used the following reasoning. The isotopic composition of the plant water is determined by the water uptake of the plant over several layers of soil water by the following equation:

$$\delta\mathrm{Pl} = \sum_{i=1}^{m} n_i \times \delta_i \qquad (1)$$

where δPl is the isotopic composition of plant stem water, n_i is the proportion of water uptake at the ith level relative to the water uptake at all levels and δ_i is the isotopic composition of soil water at ith level. Some studies have used the relative water content of the soil at each level as n_i (Dawson, 1998, for example). We chose, however, not to use this simplification since n_i is not only a function of relative water content, but of root abundance and functionality at each level of the soil profile. For the deuterium treated plots, the same equation holds; we denote the isotopic composition of plant stem water in the treated

plots by the following equation:

$$\delta'\mathrm{Pl} = \sum_{i=1}^{m} n_i \times \delta'_i \quad (2)$$

where δ'Pl is the isotopic composition of plant stem water in the treated plots and δ'_i is the isotopic composition of soil water at ith level in the treated plots. We assume here that there is no difference in the proportion of plant water uptake at any particular depth in the soil profile between treated and control plots. We can estimate the minimum water uptake by plants at the labeled region in the soil where the water is more enriched than that in the control plots by the following reasoning. For simplicity of analysis, assume that the only difference between the isotopic values of soil water of treated and control plots is at the depth interval k, where the deuterium enrichment is the highest in the treated plots. We can then modify Equations (1) and (2) to the following:

$$\delta\mathrm{Pl} = n_k \times \delta_k + \sum_{i=1}^{k-1} n_i \times \delta_i + \sum_{i=k+1}^{m} n_i \times \delta_i \quad (3)$$

$$\delta'\mathrm{Pl} = n_k \times \delta'_k + \sum_{i=1}^{k-1} n_i \times \delta_i + \sum_{i=k+1}^{m} n_i \times \delta_i \quad (4)$$

respectively. Subtracting these two simultaneous equations we derive the following equation giving the proportion n_k of water uptake from k depth interval in the soil profile.

$$n_k = \frac{(\delta'\mathrm{Pl} - \delta\mathrm{Pl})}{(\delta'_k - \delta_k)} \quad (5)$$

It is apparent that n_k is a measure of minimum proportion of water uptake by plants in the labeled region. If plants were taking water from any other part of the enriched region, they would have to be taking a greater proportion than n_k. This is because the regions other than the peak (k depth) would have a lower deuterium enrichment and by mass balance principles, a greater proportion of water from these regions would need to be present in order to account for the deuterium enrichment in plants found in the treated plots relative to those in the control plots. These proportions may be expressed as percentages after multiplying by 100.

For the calculations of minimum percentage water uptake by samples collected 3 days after irrigation, we only used δD values of control trees (the only control) harvested at that time. We estimated that the error of using trees as the representative on this particular sampling date is small because no substantial difference in natural abundance between trees and lianas was previously observed (less than 10‰); neither were any differences noted between forest and pasture plants from previous measurements. In the treated plots, however, differences between δD values of water from lianas and trees were in the range of 30‰ at that time. For subsequent sampling dates, we compared the treated plant samples in the forest with the average of control trees and lianas because of small sample size. Shrubs and grasses in the pasture were compared with their respective control values.

Root distribution in the pasture

Because of its low species diversity compared to the forest ecosystem, root distribution of plants with different photosynthetic cycles in the abandoned pasture area could be investigated by root biomass' carbon isotope ratio. One liter of soil was collected every 0.25 m down to 1 m depth and every 0.5 m down to 4 m for three replicate cores. Soil samples were soaked in water to loosen root-soil aggregates; water was agitated and then decanted into a sieve of 0.85 mm (mesh #20). Soil was subjected to three such washing cycles. Root collected in those samples were dried in paper bags first in the sun, and later in a laboratory oven before being weighed in two separated fractions. The coarse fraction containing roots larger than 2 mm in diameter was not used in the analysis. Carbon isotopic analysis was performed only on fine root samples.

Root data treatment

We used the δ^{13}C of root material throughout the soil profile to calculate the root mass from C_3 plants (mostly *S. crinitum*) and C_4 plants (mostly *P. maximum*). Previous measurements of stem tissue from these species gave δ^{13}C values of -12.0 ± 0.07‰ (mean $\pm$ SEM, PDB) for the grass *P. maximum* and -28.5 ± 0.15‰ (PDB) for the shrub *S. crinitum*. These are typical values for C_4 and C_3 plants, respectively (Deines, 1980).

The weight of the root mass for each group at a particular depth in the soil profile was calculated as follows. Three cores were initially collected but because of large variation of root mass these cores were merged and analyzed as a single non-replicated sample. We then calculated the proportion of each

group in the root sample by the following equation:

$$\delta_{\text{root}} = n\ .(\delta_{C3}) + (1 - n)\ .(\delta_{C4}) \quad (6)$$

where δ_{root} is the weighted average fine root carbon isotope composition. For this reason, the results are shown without standard error estimates.

The weight of roots from each functional group was then calculated by the following equations:

$$W_{\text{C3plant roots}}\ (\text{mostly } S.crinitum) = n\ .\ (\text{root weight}) \quad (7)$$

$$W_{\text{C4plant roots}}\ (\text{mostly } P.maximum) = (1 - n)\ .(\text{root weight}) \quad (8)$$

Sample preparation and isotope analyses

Soil and plant samples either for natural abundance or labeled water study had water extracted by vacuum distillation in a specially designed line that allowed us to process six sample batches twice a day. The water samples were converted to hydrogen gas before mass spectrometry analysis by the uranium method (Bigeleisen et al., 1952) for natural abundance study or by zinc for labeled samples (Coleman et al., 1982). The zinc method reduces individual samples to hydrogen in separate vials thus completely avoiding potential cross-contamination; it is also faster than the former.

For the carbon isotope analysis of the root material, fine roots were ground and burned for 4–5 h at 800 °C in evacuated 9-mm Vycor sealed tubes containing a cupric oxide and copper mixture (Boutton, 1991; Lin and Sternberg, 1992). The resulting gaseous carbon dioxide was cryogenically purified in a vacuum line prior to analysis.

The precision for hydrogen analysis in the mass spectrometer was ± 2‰; results were expressed in delta notation against the SMOW. For carbon analyses, the precision was ± 0.1‰; results were expressed *versus* PDB.

Results

Natural isotope abundance of the soil profile

Figure 1 compares the variation of the δD in the soil water profile to the average isotopic values of plant stem water for both forest and pasture in November 1994. It shows that soil surfaces (δD = −3‰) are naturally enriched in relation to deeper layers of the soil. Soil water isotopic values are less enriched at 1 m depth but increase at lower depths. The sigmoidal pattern of variation for the isotopic contents of soil water observed here has been reported previously (Le Roux et al., 1995; Schulze et al., 1996; Weltzin and McPherson, 1997).

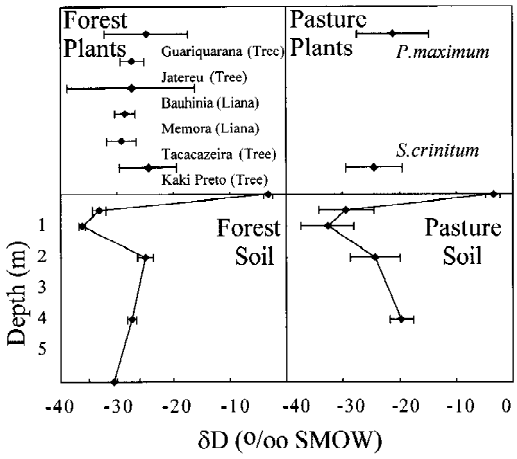

Figure 1. Natural δD values (mean ± SD) of plant stem water and of the soil water profile in the primary forest and an abandoned pasture in Paragominas (Pará, Brazil). Samples were collected on November 1994.

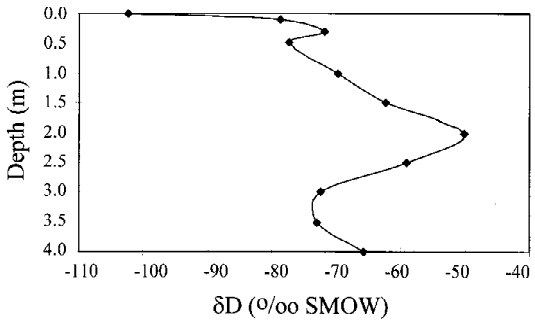

Figure 2. δD values of water in the soil profile from a control core taken during the 1996 wet season a few days before label introduction in the soil profile.

The analysis of natural abundance of deuterium in stem water from forest and from pasture plants indicated that values obtained for tree species did not differ from that of lianas, neither was there a significant distinction between the two species in the pasture (forest plants: F = 0.2695, P = 0.92; pasture plants: F = 0.9367, P = 0.361). The average values in the forest and in the pasture were similar (F = 0.740, P = 0.641). The average values for forest plant water (δD = −27‰) corresponded to that of three different depths

of the soil profile (0.5, 1.8 and 4 m deep). The averages for pasture plant water ($\delta D = -23‰$) matched the isotopic composition of two different depths of the soil profile (0.5 and about 3 m deep). Isotopic composition of stem water from forest plants could also be arrived by an infinite number of possible combinations of water uptake depth.

Labeling experiments

Label movement in the soil

Because of very light isotopic values in the precipitation water during the 1996 wet season compared to that observed in 1994, control δD values at the surface of the soil profile was $-100‰$ and increased to an almost constant δD value of $-70‰$ down to 4 m depth (Figure 2). In contrast, soil surface in the treated plots 3 days after label introduction showed deuterium enriched water with a mean δD value of $+121 \pm 25‰$. The mean difference between δD of water in the soil profile of treated and control plots 3, 8 and 14 months after irrigation for primary forest and for pasture are shown in Figure 3. Three months after irrigation (end of 1996 wet season), a peak of labeled water 75‰ heavier than soil water from control cores developed at 0.60 m depth in the forest, spreading from the surface down to 2.00 m (Figure 3A). The pasture peak was broader with a δD value 59‰ greater than that observed in the control cores and between 0.40 and 1.00 m deep, but the level of enrichment between the forest and the pasture was very similar based on area integration of δD *versus* depth (Figure 3A, D). It is apparent that considerable deuterium was lost when the peak δD values 75 and 59‰ above the control core values are compared to that of the initial application of $\sim$+71 300‰. The dilution factor would be about 1000 fold in this case. This dilution was probably because of losses by evaporation and also by plant uptake during the last fourth of the 1996 wet season. The study by Araguás-Araguás et al. (1995) also corroborated this large initial dilution of labeled water in the soil. Figure 3A, D also show δD values of soil water from cores 0.5 m outside the plots. δD values were typically between $\pm$ 10‰ compared to those observed in the control plots.

Five months later, at the end of the dry season, soil water label enrichment above the control core values decreased by 47% in the forest plots, whereas in the pasture this reduction was only of 20% (Figure 3B, E). The label peaks were still at 0.60 m depth but their shapes had become more symmetric. After 14 months, both forest and pasture soil profile had peak δD values in the range of 25–30‰ above control values, but the pasture peak migrated further on the soil profile than the forest peak.

Area integration of the soil water profile curves indicated equal label loss for forest and pasture up to eight months after labeling. However, there was 32% drop in the label concentration in the forest plot after the 1997 wet season, 14 months after irrigation (Figure 3C), whereas no further decrease in label concentration was observed for the pasture (Figure 3F).

Plant results and water uptake patterns

δD values of stem water from control plants three days after irrigation closely reflected the isotopic values of soil water at that time showing an average δD value of $-78 \pm 2‰$ (Table 1). Forest trees in the treated plots had stem water with an average δD value of $-72 \pm 3‰$ which was not significantly different from that of control plants, whereas lianas had stem water significantly more enriched than control plants ($-42 \pm 13‰$, $P<0.01$, Student-*t* test). This indicates that lianas were acquiring substantial labeled water from the soil surface in the irrigation plot 3 days after irrigation.

In the pasture, the colonizer shrub *S. crinitum* showed an enrichment similar to that of the lianas ($\delta D = -44 \pm 3‰$) and *P. maximum* plants presented the highest enrichment ($\delta D = -2 \pm 18‰$, Table 1). Both species had stem water significantly more enriched than that of control plants indicating substantial labeled water uptake within the irrigated plots by both species in the pasture ($P<0.01$, Student-*t* test).

After the initial pulse of deuterated water, δD values of stem water from forest trees showed significantly greater deuterium enrichment than that of control trees 3 ($P<0.05$), 8 and 14 months after irrigation ($P<0.01$), whereas lianas showed significant differences from control lianas only 8 months after irrigation at the end of the dry season ($P<0.01$). In the pasture, δD values of stem water from *S. crinitum* were not significantly different from that of control plants at 3, 8 and 14 months after irrigation. δD values of *P. maximum* water in the treated plots were significantly higher ($P<0.01$, Student-*t* test) than that of the control plot plants throughout the experiment except for 14 months after irrigation, when the label peak was below 1 m depth.

Using Equation (5), we calculated the minimum water uptake within the label peak region for each of the plant groups (Figure 4). Minimum percentage of water uptake increased throughout the experiment as

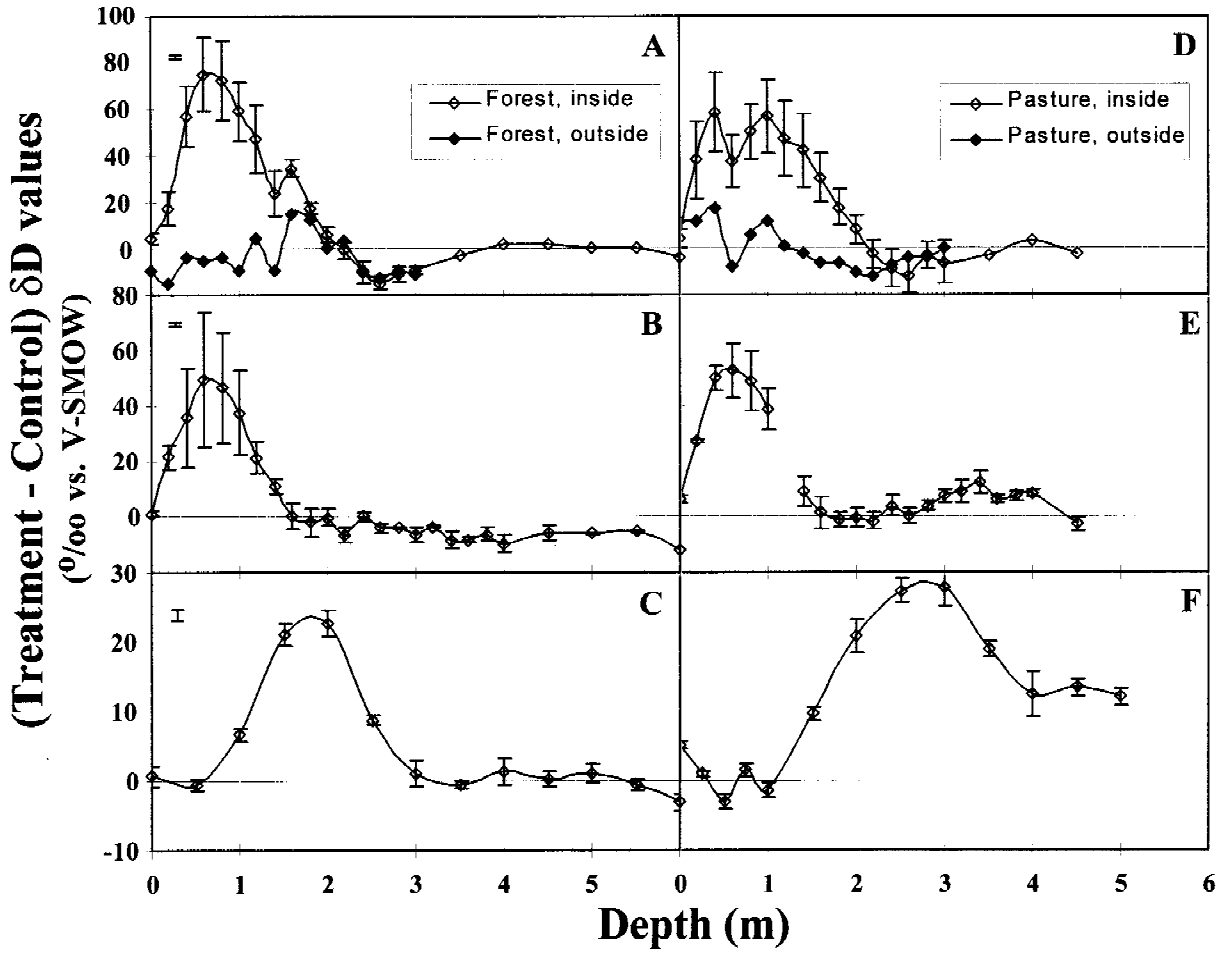

Figure 3. Average differences (± SEM) in δD water values between treated and control plots in the forest soil (A, B, C) and in pasture soil (D, E, F) profiles at different dates. Trivial loss of label water by lateral movement outside the irrigation plots is shown three months after surface irrigation (full symbols in A and D). Eight months after irrigation the deuterium peaks have not moved down from previous sampling (end of dry season, B and E). One wet season later, or 14 months after soil irrigation, the label peak is 1.80 m deep in the forest and 3.00 m deep in the pasture (C and F).

the label peak moved down the soil profile for forest trees, whereas for lianas, it remained relatively constant. In the pasture, the grass also showed a relatively constant value for the minimum percentage of water uptake in the first 8 months, whereas for the shrub, *S. crinitum*, the minimum percentage decreased to an insignificant level just 3 months after irrigation.

Root distribution in the pasture soil profile

Calculation of root mass using $\delta^{13}C$ values indicated that the roots of C_4 plants, including grasses, principally occupy the top 2 m of the soil profile (Figure 5). The bulk of C_3 plants roots which includes *S. crinitum* roots, on the other hand, were distributed in the top 0.25 m in the soil profile.

Discussion

Two major conclusions regarding the study of water uptake by plants can be drawn from our observations using natural stable isotope abundances. First, the results show that the natural variation in stem water isotopic values for different species (as well as for the soil profiles in nearby locations having different vegetation) is low. Second, the results also confirm that in the cases studied here the variation in the natural abundance of isotopes in the soil profile water is

Table 1. Mean water δD values (± SEM) from control and treated plants in different seasons. For the 1996 wet season, all plants in treated plots were compared only with trees in untreated area

Season	Plant	Control δD (‰ SMOW)	*n*	Treatment δD (‰ SMOW)	*n*	Sig. level	Months after irrigation
April 1996	Tree	-78 ± 2	9	-72 ± 3	14	n.s.	(3 days)
During Wet	Liana	-78 ± 2	9	-42 ± 13	6	**	
	P.max	-78 ± 2	9	-2 ± 18	2	**	
	S.crin	-78 ± 2	9	-44 ± 3	4	**	
July 1996	Tree	-28 ± 6	10	-11 ± 4	22	*	3
End of Wet	Liana	-19 ± 9	3	-15 ± 5	12	n.s.	
	Mean	-26 ± 5	13				
	P.max	-19 ± 2	4	$+2 \pm 2$	8	**	
	S.crin	-26 ± 3	4	-26 ± 2	8	n.s.	
December 1996	Tree	-34 ± 2	6	-19 ± 3	23	**	8
End of Dry	Liana	-25 ± 1	3	-8 ± 7	9	**	
	Mean	-31 ± 2	9				
	P.max	-36 ± 2	4	-2 ± 4	8	**	
	S.crin	-20 ± 2	3	-19 ± 1	8	n.s.	
June 1997	Tree	-31 ± 2	5	-13 ± 2	18	**	14
End of Wet	Liana	-26 ± 1	5	-24 ± 2	6	n.s.	
	Mean	-28 ± 1	10				
	P.max	-24 ± 1	5	-25 ± 1	10	n.s.	
	S.crin	-27 ± 1	5	-30 ± 1	9	[a]	

** $P < 0.01$; * $P < 0.05$.
[a] Treatment was significantly lower than control.

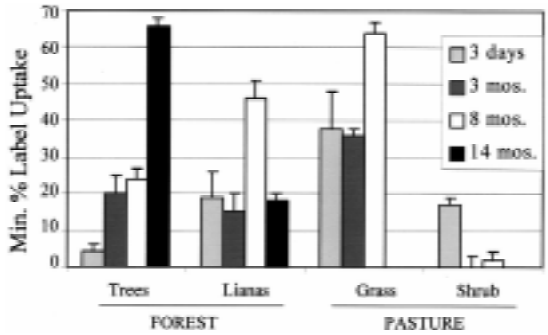

Figure 4. Calculated minimum percentage of labeled water uptake (±SEM) from the label region of the soil profile for different groups of plants in forest and in pasture plots at different times after irrigation with label water. Values not shown indicate that treatment values were not significantly enriched in deuterium relative to control plants and, therefore, percentages were not estimated.

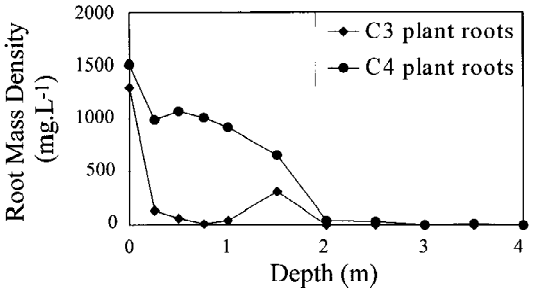

Figure 5. C_4 (including *P. maximum*) and C_3 (including *S. crinitum*) fine root distribution in degraded pasture based on carbon stable isotope analysis.

insufficient to determine depth of plant water acquisition. The reason is that the natural isotopic abundance of plant stem water may match the isotopic value of more than a single soil layer (Le Roux et al., 1995; Schulze et al., 1996; Weltzin and McPherson, 1997). Our oxygen isotope analysis of the soil profile (not shown here) indicated the same situation.

As an alternative to using natural abundance analysis of water in the soil profile, we carried out experiments with deuterated water. The soil label distribution (Figure 3) followed the expected pattern of piston flow percolation by which rain subsequent to

the label irrigation pushes the label water downward (Araguás-Araguás et al., 1995). For the first 3 months after irrigation when the label was still close to soil surface, evaporation could have had an effect on differences in label quantity between the forest and the pasture plots. However, a comparison of the curve areas showed that the forest label quantity was only about 5% higher than that of the pasture. The broad pasture label peak recorded 3 and 14 months after irrigation suggests the possibility of macropore movement of the water in the soil (Nepstad, pers. obs.). Carvalheiro and Nepstad (1996) found a higher frequency of 'soft spots' in pasture soil profiles than those of the forest. These soft spots may provide channels by which the label can flow rapidly. As seen in Figure 3E, part of the label water had actually percolated faster than the main peak in the pasture plots after eight months. Deep soil layers in the pasture may have high water content (Nepstad et al., 1994) which could also cause higher percolation rates. The label, therefore, tended to spread vertically more in the pasture than in the forest (Figure 3D). Sub-surface lateral flow capable of moving the labeled water outside the treated plots was minimum as shown by the cores drilled just outside the plot areas 3 months after irrigation (Figure 3A, D). There was at most 10‰ difference in soil water between cores just outside the plots and the control cores. Despite these differences in label movement between forest and pasture plots, the amount of label was similar in both environments after 3 months.

Lack of rainfall during the dry season resulted in no downward movement of the label in the soil, as observed in Figure 3B, and 3E for samples collected 8 months after label introduction. The label peak declined from 75 to 50‰ above control core values during the dry season in the forest. The simultaneous peak reduction in pasture plots was only from 59 to 53‰ above control core values. The narrower and shallower distribution of label on the pasture plots compared with that sampled 3 months after irrigation may represent sampling variation as a result of a more heterogeneous soil structure found in the pasture (Carvalheiro and Nepstad, 1996). The decrease in label values represent both equilibration with and losses to the atmospheric vapor. By December 1996, 8 months after irrigation, the label remained largely within the top meter of the soil profile in both environments. The peaks, however, became well defined at 0.6 m depth in both environments, spreading down to 1.60 m depth. Although drier than usual (1145 mm), the 1997 wet season rainfall was able to push the label downward to a depth where soil water evaporation was unlikely. Fourteen months after irrigation, just after the 1997 wet season, the label δD values once again decreased in the forest plots. Because evaporation is an unlikely cause of label loss, we assumed that this decrease was attributable to plant uptake together with dilution by rainfall. The forest labeled water was then located at 1.80 m deep, and the peak shape became very symmetric without significant enrichment in the soil's top meter (Figure 3C). Integration of the label profile in the pasture indicated that no further reduction in label levels occurred from 8 to 14 months after irrigation. This suggests that minimum water uptake was occurring below 1 m depth. The pasture peak present on December 1996 (Figure 3E) moved down to 3.00 m depth (in contrast to a migration to 1.80 m in the forest) and extended to deeper layers (Figure 3F). The label in the pasture spread from 1 to 5 m depth by the time of the conclusion of the experiment.

The absorption of label by plants is a function of both the depth at which the label occurs, and the spatial distribution of the plant's absorptive root system.

Our interpretation of plant water uptake in this experiment is limited to uptake within irrigated plots. This limitation is caused by the possibility that plants within the treated plots extend their roots outside the treatment area causing a dilution of the label.

Calculations of the minimum percentage of water uptake within the label region 3 days after irrigation suggest that trees in the forest either did not readily acquire water from the soil surface within the irrigated plot as much as lianas did (4 vs. 19%, respectively) or there is a greater lag period between water uptake and its appearance in stem tissue (i.e. sap flow is lower for trees compared to lianas). Because the label peak was very close to the surface at that time, the minimum percentages observed indicated that lianas may have a greater proportion of functional water absorbing surface roots within the plots compared to trees. Forest trees, however, increased the minimum percentage of water uptake to 20% as the peak migrated downward in the soil profile, 3 and 8 months after irrigation (Figure 4). As the label peak moved down after the 1997 wet season, forest trees increased their minimum percentage of water uptake from the label region from 24 to 66%, which indicates substantial activity of roots in the irrigated plots below the top meter of forest soil.

Although lianas more quickly acquired label just after irrigation, they had a relatively constant minimum percentage of water uptake from the label region

as the label peak migrated downward. With the exception of minimum percentage uptake measured 8 months after plot irrigation (December), the values remained close to 20% throughout the experiment. This indicates that within the treated plots functional liana roots may be more homogeneously distributed in the soil profile than tree roots. The sharp increase in minimum percentage of water uptake from the label region for lianas during the dry season (December), when the surface layer of the soil is the driest, may have been caused by little water uptake at the surface soil layer by lianas and a greater reliance on the moister soil layers 1 m deep where the label was found.

The minimum percentage of water uptake from the label region by grass was higher than that by trees, lianas and shrubs just after the label application, as well as 3 months later. Toward the end of the experiment (14 months after irrigation), however, grasses ceased to take up a significant quantity of labeled water which suggests that 2 m may be their limit of water uptake, in contrast to forest trees that continued to increase their water uptake. During the dry season, the water uptake pattern of *P. maximum* resembled that of lianas with a sharp rise in the minimum percentage of uptake from 36 to 64% (Figure 4). Like lianas, grasses may be able to vertically shift their water source depending on the season. After the 1997 wet season, *P. maximum* showed no enrichment in its sap water indicating that it was not accessing the labeled water below 1.00 m depth.

The striking result of this analysis was that the shrub *S. crinitum* stopped acquiring labeled water as soon as the label moved to 1 m depth below the surface (Figure 3D). *S. crinitum* showed no enrichment three months after irrigation and only a weak signal 5 months later. No label was found in the shrub stem water 14 months after labeling. Our hypothesis that *S. crinitum* is able to invade abandoned pasture because of a capacity to take up water from deep, moist soil layers in the pasture is, therefore, refuted. Instead, *S. crinitum* seems to acquire the shallow water resource during wet periods and has an ability to survive during long dry periods. We note that gas exchange characteristics of *S. crinitum* are typical of stress tolerant plants (Dias-Filho and Dawson, 1995). *S. crinitum*'s acquisition of water may also be explained by widespread surface roots, but we did not assess this. The water uptake pattern of *S. crinitum* may be essential to forest regeneration processes in abandoned pastures of the eastern Amazon, because shrubs are important perch sites for frugivorous birds and bats which can enhance forest species recruitment in the pasture (Nepstad et al., 1991; Silva et al., 1996; Vieira et al., 1996).

Our analysis of root distribution in the soil profile corroborates our observation on water uptake patterns in the abandoned pasture. C_3 plants including *S. crinitum* had the bulk of its roots very close to the soil surface ($\sim$0.25 m), as indicated by the stable carbon isotope analysis (Figure 5). C_4 plants including *P. maximum*, on the other hand, had a more homogeneous root distribution over the top two meters of the pasture soil. No significant fraction of fine root from either plant group was found below 2 m depth in the soil profile. This observation was confirmed by the rapid drop off in label uptake by the shrub as labeled water moved down the soil profile, and by the maintenance of high label uptake by the grass until the deuterium label had dropped to beneath 2 m depth.

These sequential 'snapshots' of the belowground processes observed here indicate that, within the limitations of our interpretation, plant functional groups are exploiting specific soil volumes. The results confirm the hypothesis that forest trees can obtain water from depths below 1 m in the soil. Water uptake by the lianas studied here may operate in a more opportunistic manner than uptake by the trees, taking advantage of brief rainfall events. As with lianas, the water uptake behavior of grasses seemed to respond to seasonality with an increase in the proportion of water uptake from deep layers of the soil during the dry season.

Water partitioning in the pasture does not conform to Walter's niche partition hypothesis (Walter, 1979), by which grasses absorb water from the soil's top meter, while woody plants take up water deep in the soil (Scholes and Walker, 1993; Weltzin and McPherson, 1997). We observed the most abundant woody species (*S. crinitum*) absorbing water only from the top 0.25 m layer of the soil profile. This may demonstrate how the early stage of pasture invasion by these colonizers functions, with shrubs investing in fast water uptake from the soil surface during the wet season.

Isotope techniques used here elucidated different patterns of water uptake between primary forest and abandoned pastures. Vertical soil water movement was faster in a pasture than in forest. Because less label was lost in the pasture than in the forest, we hypothesize that differences in percolation rates are because of greater water saturation of pasture than forest soils during the dry season resulting from limited plant water uptake. These observations are consistent with

observations by Nepstad et al. (1994) using a mass balance approach at the same site.

The introduction of the labeled water into the soil elucidated the depth of plant water uptake in the eastern Amazon for plant transpiration, which in turn was shown to be the major source of water vapor coming from the forest during the dry season (Moreira et al., 1997). By determining the time of water acquisition, the pulse-chase technique has refined certain hydrological parameters, such as soil water storage, in global climate models (Schulze et al., 1996; Waring and Schlesinger, 1985). Although the water cycle in the Amazon has been well studied on a large scale, small particularities of the water cycle must be understood because of the importance of ecophysiology and community structure in determining climate changes on a broad scale (Broecker, 1996).

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