

Uptake of water by lateral roots of small trees in an Amazonian Tropical Forest

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Received 9 January 2001. Accepted in revised form 22 September 2001

Key words: deforestation, edge effects, root structure, stable isotopes, tropical forests, water uptake

Abstract

A pulse chase technique was used to determine depth and breath of plant water uptake in an Amazonian evergreen forest. Two 2×2 m² plots were irrigated with deuterated water. The deuterium pulse, measured as δD values of soil and plant sap water, was followed in the soil water profile and in stem water of small trees inside and up to 12 m away from the irrigated plots. The deuterium pulse percolation rate was measured to be approximately 0.25 m/month and similar to a previous study in central Amazon. There was little horizontal movement of label through the soil profile; allowing us to conclude that any evidence of label in plants away from the irrigation plots implies the presence of their roots inside the irrigation plots. The bulk of label uptake occurred in plants inside the irrigation plots. However, there were a few individuals as far as 10 m away picking up the label from the irrigation plots. This labeling pattern leads to the conclusion that small trees may have a core of water absorbing roots close to their main trunk, with some roots meandering far from their main trunk.

Introduction

Edge effects in tropical forests are becoming increasingly important with deforestation rates presently exceeding 15×10^6 ha/yr (Whitmore, 1997). Edge effects include changes in species composition (Janzen, 1983; Laurance, 1991, 1998; Laurance et al., 1997), changes in water relations (Kapos, 1989), and loss of biomass (Laurance et al., 1997). The underlying cause for several edge effects may be changes in water relations. Kapos (1989) observed that temperature and vapor pressure deficit (VPD) increased at forest edges leading to higher demand of water by plants as much as 40 m from the forest edge. In addition, increased light and wind penetration at the edge of a forest can intensify plant water demand. Higher water demand and wind speeds contribute to higher mortality and tree-fall with

replacement by other functional groups at the forest edge (Laurance et al., 1997; Laurance, 1998). It has been proposed that because of higher wind disturbance at forest edges, there should be a shift towards disturbance adapted functional groups such as successional trees and lianas at forest edges (Laurance et al., 1997).

Although much is known about above ground water relations at forest edges, little is known about underground processes. To more accurately predict the consequences of edge effects, it is necessary to understand depth and breath of soil resource exploitation by roots. Stable isotope techniques provide an important tool to our understanding of root processes (Dawson and Ehleringer, 1991; Ehleringer et al., 1991; Ewe et al., 1999; Jackson et al., 1995; Lin et al., 1996; Meinzer et al., 1999; Sternberg et al., 1991, 1998; White et al., 1985). Because there is no isotopic fractionation during plant water uptake by most plants (Dawson and Ehleringer, 1993; Wershaw et al., 1970; but see Lin

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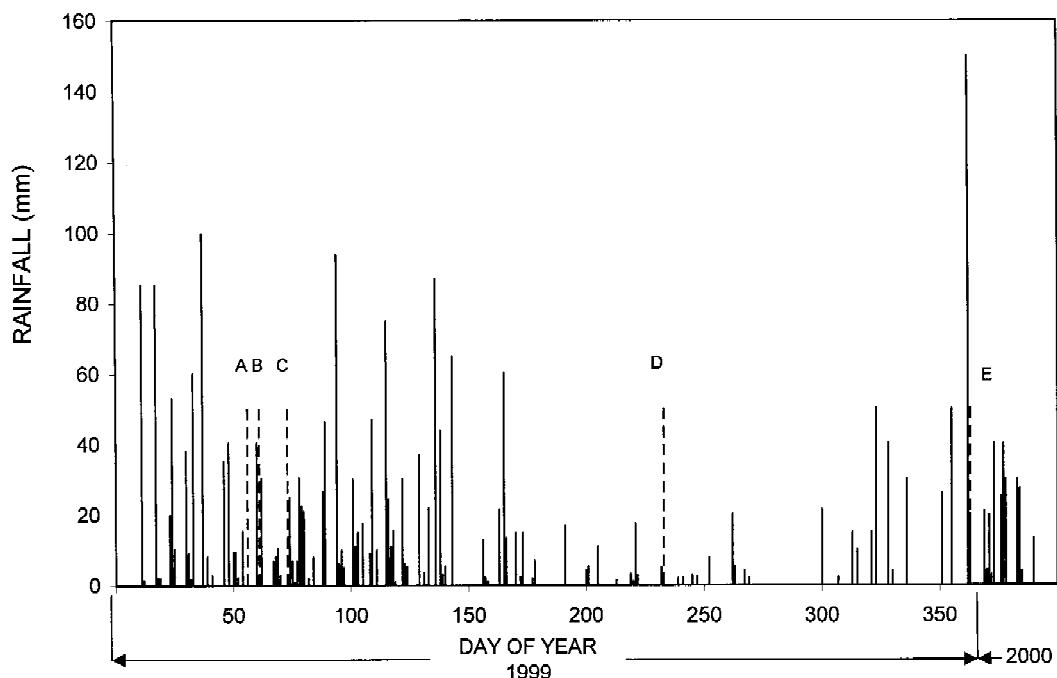


Figure 1. Daily precipitation at the *Floresta Nacional Tapajos* from January 1999 through January 2000. Dashed lines represent the time of: (A) irrigation of plots with deuterated water, (B) first sampling 3 days after irrigation, (C) second sampling 15 days after irrigation and (D and E) third and fourth sampling 182 and 311 days after irrigation, respectively.

and Sternberg, 1993 for some exceptional cases) and soil or ground water can show isotopic heterogeneity in the profile, it is possible to use stable isotope ratios of plant stem water as a natural tracer of soil water uptake. However, if the isotopic composition of water in the soil profile is redundant, i.e. different depths show the same isotopic composition (see Moreira et al., 2000), natural stable isotope ratios cannot be used. Labeling of the soil water profile with deuterated water is better suited to trace plant water uptake in this situation (Moreira et al., 2000; Plamboek et al., 1999). Another situation where isotopic labeling is more suitable is in tracing horizontal exploitation of soil water resources by plants. Although the isotopic composition of soil water may show vertical heterogeneity, it most often is horizontally homogeneous. Here, we determined horizontal and vertical water exploitation by roots of small trees in an Amazonian forest by using a pulse chase technique (Araguás–Araguás et al., 1995; Moreira et al., 2000). A pulse of deuterium oxide was applied as a tracer and followed in the soil profile and in stem water of small trees.

Materials and methods

Site

Experiments were carried out in the *Floresta Nacional de Tapajos* (State of Para, Brazil, Lat $2^{\circ} 53' 49''$, Long $54^{\circ} 57' 07''$) located about 50 km south of the city of Santarem. The forest is characterized as broad leaf evergreen with a seasonally high rainfall period starting in December and ending in August followed by a dry season (Figure 1). Total annual rainfall in this region averages 1700 mm. Soils at this site are highly weathered tertiary sediments (Haplustox), dominated by Kaolinite clays.

Two 2×2 m² plots were selected for irrigation with deuterated water. In each treatment plot and surrounding area we identified, measured trunk diameter at breast height (dbh), tagged, and mapped four to five individuals inside the irrigation plot and groups of 5 replicate individuals each approximately 0–3, 3–6, 6–9, 9–12 m away from the irrigation plot (Table 1). Average dbh ($\pm \sigma$) of treatment trees was 71 ± 41 mm. Ten individuals with comparable dbh, averaging 113 ± 35 mm, were chosen in a control area approximately 200 m away from treatment plots. Because of the high diversity typical of tropical ecosystems, it was not

Table 1. Species of small trees and saplings sampled in the treatment site, their diameter at breast height (cm) and distance class from the two replicate irrigation plots

Plot A			Plot B		
Species	d.b.h.	dist. class	Species	d.b.h.	dist. class
<i>Ampelocera edentula</i>	4.0	inside	<i>Coussarea ovalis</i>	4.0	inside
<i>Amphirrhox surinamensis</i>	3.3	"	<i>Coussarea racemosa</i>	4.0	"
<i>Endopleura uchi</i>	2.9	"	<i>Licaria membranacea</i>	3.0	"
<i>Protium apiculatum</i>	11.5	"	<i>Myrciaria floribunda</i>	12.7	"
			<i>Pausandra arianae</i>	2.8	"
<i>Eschweilera pedicellata</i>	4.7	0–3 m	<i>Amphirrhox surinamensis</i>	3.1	0–3 m
<i>Myrciaria floribunda</i>	22.0	"	<i>Amphirrhox surinamensis</i>	2.5	"
<i>Tachigalia paniculata</i>	4.2	"	<i>Coussarea micrococca</i>	5.5	"
<i>Talisia cerasinae</i>	4.7	"	<i>Coussarea racemosa</i>	6.0	"
<i>Virola michelii</i>	5.7	"	<i>Duguetia echinophora</i>	8.0	"
<i>Cupania scrobiculata</i>	5.9	3–6 m	<i>Coussarea racemosa</i>	4.4	3–6 m
<i>Licania membranacea</i>	4.7	"	<i>Coussarea racemosa</i>	4.7	"
<i>Manilkara huberi</i>	3.4	"	<i>Coussarea racemosa</i>	4.0	"
<i>Protium robustum</i>	4.0	"	<i>Eschweilera pedicellata</i>	6.2	"
<i>Talisia pedicellaris</i>	7.6	"	<i>Poecilanthe effusa</i>	8.4	"
<i>Coussarea ovalis</i>	6.3	6–9 m	<i>Brossimum guianense</i>	7.0	6–9 m
<i>Eschweilera pedicellata</i>	12.7	"	<i>Coussarea macrophylla</i>	12.0	"
<i>Geissospermum velozii</i>	3.7	"	<i>Coussarea racemosa</i>	7.5	"
<i>Pouteria trichopoda</i>	6.8	"	<i>Gustavia poeppigiana</i>	11.0	"
<i>Talisia retusa</i>	3.7	"	<i>Talisia cerasina</i>	5.7	"
<i>Calyptanthes lucida</i>	4.2	9–12 m	<i>Aiouea densiflora</i>	8.4	9–12 m
<i>Coussarea racemosa</i>	11.3	"	<i>Coussarea racemosa</i>	10.5	"
<i>Coussarea racemosa</i>	19.9	"	<i>Coussarea racemosa</i>	5.2	"
<i>Planchonella pachycarpa</i>	10.0	"	<i>Licaria armeniaca</i>	11.2	"
<i>Pouteria macrophylla</i>	11.7	"	<i>Poecilanthe effusa</i>	7.7	"

possible to replicate treatments within a single species in a consistent and statistically useful manner.

Irrigation

Each treatment plot received 5 L of water having 30% (volume) 99.8% deuterium oxide and 70% of water having background deuterium levels (about –20%). This was followed by 20 L of water having background deuterium levels. Leaf litter was raked out of the plots before sprinkling of labeled water and raked back into plots after label application. Label was applied during the wet season (Figure 1) to maximize label percolation rate and therefore minimize loss of label by evaporation and equilibration with

ambient forest vapor. Water added to treatment plots constitutes only about 0.4% of the total annual rainfall during the experimental period (1801 mm), and should not have impacted plant water relations in treatment plots compared to that of the control plot.

Water extraction and isotopic analysis

Deuterium levels were measured in stem water of trees and water in the soil profile through time (Figure 1). At each sampling, two or three replicate soil cores were taken in each treatment plot, and the control area, and one core was taken 0.5 m outside each treatment plot with an AMC (Forestry Supplies) soil auger having a diameter of 0.10 m. Soil cores were taken to a depth

of 0.6, 1.0, 3.0 and 5.0 m on March 2, 14, August 28, 1999 and January 4, 2000, respectively. Soil aliquots of approximately 20 g were collected at depth intervals of 0.2 m or 0.5 m, sealed in glass tubes and taken to the laboratory for distillation of water and isotopic analysis. A well-suberized plant stem sample about 100 mm long with an approximate diameter of 8 mm from each selected tree was collected at each sampling date and sealed in tubes for distillation and isotopic analysis as in soil samples.

Water samples were extracted by cryogenic distillation in the laboratory (Moreira et al., 2000), sealed in a glass ampoule with zinc and heated for 2 h at 500 °C as in Coleman et al. (1982). Hydrogen gas was analyzed on a Micromass Prism Isotope Ratio Mass Spectrometer with a precision of $\pm 0.5\text{\textperthousand}$. All values are reported here as δD values where:

$$\delta\text{D}(\text{\textperthousand}) = \left(\frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} - 1 \right) \times 10^3 \quad (1)$$

R represents the molar ratio of deuterium to hydrogen (D/H). The standard water used here is Standard Mean Ocean Water (SMOW).

Data analysis

Isotope ratios of water from soil cores of both treatment plots were merged because there were no significant differences between the two treatment plots, and plotted as the averages at each depth for both plots. Isotope ratios of stem water from individual plants were compared to the average of the control plants using Sokal and Rohlf (1995) method of comparing a single observation with the mean of a control population. We also compared the means of the δD values of stem water from plants at different distance classes with that of the control group using a *t*-test (Sokal and Rohlf, 1995). All statistical tests were done on the arcsine transformation of the square root of the absolute D/H values of each sample. The D/H values were derived by back calculation from the measured δD values with Equation (1).

Results

Movement of label in soil

Three days after irrigation of treatment plots, when the label was still close to the soil surface (Figure 2), the deuterium peak concentration in the soil water decreased by 99% to only 0.32% deuterium (or

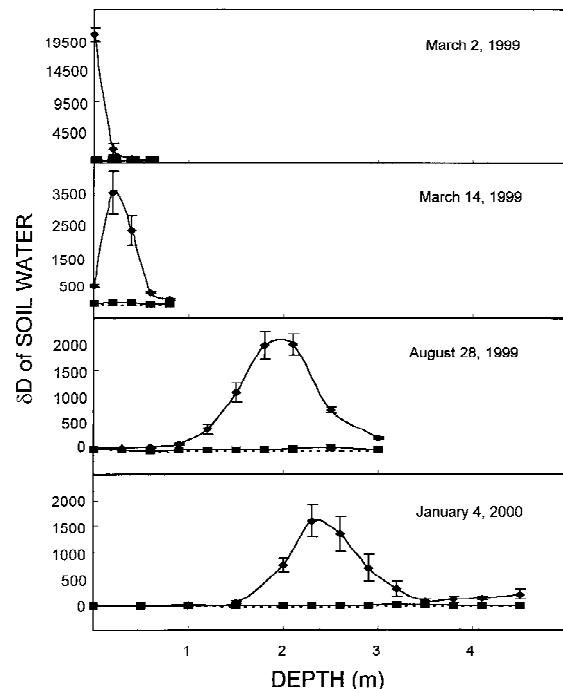


Figure 2. Hydrogen isotope ratios (δD values) of soil water in the treatment plots at different depths 3, 15, 182 and 311 days after irrigation of plots with deuterated water. Values represent the average of soil cores taken in both replicate plots ($\pm\sigma\bar{x}$). Symbols are (\blacklozenge) for soil cores taken inside the irrigation plot, and (\blacksquare) for soil cores taken 0.5 m away from irrigation plot. Dashed line represents values observed for control cores. Note the change in the vertical scale through time.

an average δD value of 19500‰). We assume that much of the deuterium was lost by equilibration with ambient vapor or by evaporation. Fifteen days after irrigation, the deuterium concentration decreased by 78% to an average δD value of about 3500‰. Loss of label leveled out from the 15th day on, with average peak δD values of 2000‰ and 1700‰ at 182 and 311 days after label application, respectively. Although initially there was a large loss of label, the remaining deuterium concentration is far above background ($-20\text{\textperthousand}$), and easily detectable by conventional isotope ratio mass spectrometry of hydrogen extracted from plant and soil water.

Uptake of label by plants

Three days after irrigation (March 2, 1999), only plants in the irrigation plots or within 3 m from the edge of the irrigation plots had levels of deuterium in their sap above background (Figure 3). Fifteen days (March 14, 1999) after irrigation, all plants within

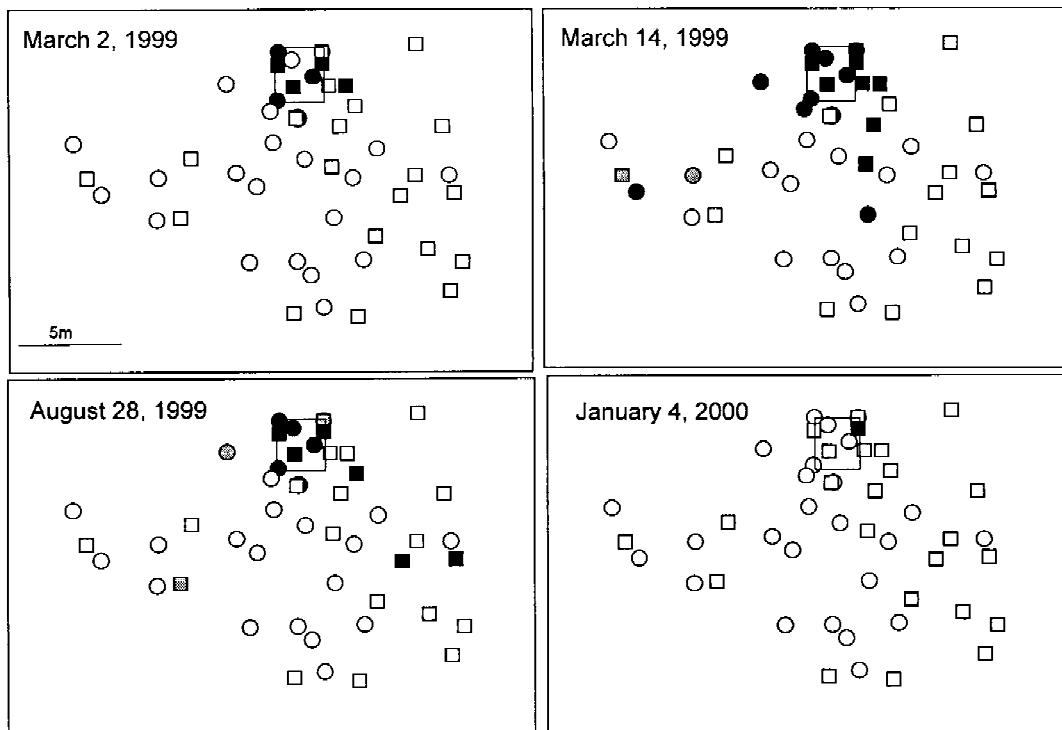


Figure 3. Location of small trees relative to their respective irrigation plot. Squares and circles represent the two replicates, respectively. Full symbols represent trees which had stem water having significantly greater deuterium content than control trees at $P<0.05$, gray symbols represent significance at $P<0.10$; empty symbols represent no significant difference between deuterium content of stem water from treatment and control plants.

the irrigation plots and 60% of the individuals outside but within 3 m of the irrigation plots were labeled. Of the individuals 3 m or more away from the irrigation plots 17% were labeled. A similar pattern was observed 182 days after irrigation (August 28, 1999) with most of the labeled plants located within the irrigation plot and a few at further distances (Figure 3). However, the number of labeled individuals at 182 days after irrigation were fewer than that observed 15 days after irrigation. Only one plant showed stem water with deuterium enrichment above background 311 days after irrigation (January 4, 2000).

Plant stem water within the irrigation plot had δD values which were 2%, 30% and 2% of the peak δD value of soil water when the peak was at the surface, 0.3 and 2 m deep, respectively (Figures 2 and 4). Although plants outside but within 3 m of the irrigation plot had significantly higher δD values compared to control plants, their δD values were substantially lower than that found in plants inside the irrigation plots. Three hundred and eleven days after irrigation, average δD values of sap water of plants for all dis-

tance classes were no different than that of control plants (Figures 3 and 4).

Discussion

The deuterium pulse percolation rate of 0.25 m/month observed here is similar to the percolation rate of 0.27 m/month measured in a central Amazonian forest (Araguás-Araguás et al., 1995), but much greater than the percolation of 0.15 m/month measured in an eastern Amazonian forest (Moreira et al., 2000) using this same technique. Percolation differences are not due to differences in total rainfall, but probably reflect differences in rainfall distribution, initial soil moisture content, soil structure and evapotranspiration, since the approximate rainfall for the above sites during the experimental period was 2455 mm, 1700 mm and 1637 mm, respectively. Label migration occurred primarily during the heavy rains of the wet season as has been observed previously at other sites. There was virtually no lateral movement of label through the soil. Samples taken only 0.5 m away from the plot edge

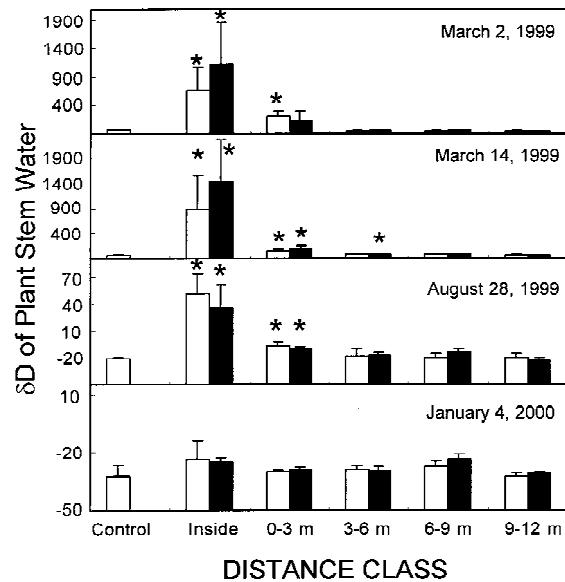


Figure 4. Average δD values of plant stem water for control individuals and for individuals at different distance classes from their respective irrigation plot. Black and white bars represent the two replicate treatments. Bars with a star indicate that the average δD values of plant water were significantly higher than that of control plants at $P < 0.05$ level. Note the change in the vertical scale through time.

had weak or no label signal (Figure 2). Therefore, any plant outside the irrigation plot showing deuterium enrichment in its sap water must be directly acquiring water from the irrigation plot. It is unlikely that labeled plants outside the irrigation plots are acquiring labeled water through mychorrhizal connections, since the fine hyphal network having labeled water would also be detected in soil samples.

Different plant labeling patterns would be expected with different root structures (Figure 5). We considered here three different types of rooting patterns and assume that there are no significant differences in rooting patterns between different species. (1) Roots of trees are mostly limited to a small core of roots associated with the main trunk. If this is the case, one would expect that only trees inside or very close to the irrigation plots would show isotopic labeling (Figure 5a). Note that if this core of roots is spread over an area with a large diameter, one would expect that plants just outside and inside the irrigation plots would have similar label quantities. (2) Trees have a system of lateral roots meandering off from the main trunk area and acquiring resources in areas far from the main trunk. The expected labeling pattern for this type of root structure would be such that labeled indi-

viduals would not cluster within the irrigation plots, but rather, they would be found spread throughout the study area (Figure 5b). (3) Plants have both a core of roots associated with the main trunk and some far reaching lateral roots. The labeling pattern expected here would be one of high label intensity in the irrigation plot with a few individuals outside the irrigation plot being labeled (Figure 5c).

The observation that all trees inside the irrigation plots were labeled during the experiment indicates, according to the examples given above, that there is a central core of water absorbing roots associated with the main stem of each individual. This central core has a limited horizontal range of soil exploitation, based on a comparison of the average δD values of plant sap water for trees just outside the irrigation plot (0–3 m) with those inside (Figure 4). If these core roots were capable of exploiting a relatively wide area of soil for water acquisition, one would expect similar label quantities for individuals inside and just outside the irrigation plot. Although average δD of plant sap water for plants just outside the irrigation plot was significantly greater than control plants on the first three sampling dates, their average deuterium levels were much lower than those inside the irrigation plots (Figure 4). For example: on March 14, the date with the highest label quantity in plant water, plants inside the two replicate irrigation plots had average δD values of 883‰ and 1443‰ while those outside the irrigation plot, but within 3 m, had average δD values of 41 and 81‰, respectively.

On the other hand, the observation that a few individuals as far as 10 m away from the irrigation plot were significantly labeled by the deuterium treatment (Figure 3) indicates that small trees can exploit soil resources far from their main stem. This supports the third hypothetical root structure shown on Figure 5c. The proportionally small number of labeled individuals far from the irrigation plot despite their long-range root structure is expected based on the following reasoning. A $2 \times 2 \text{ m}^2$ square area comprises 14%, 3.5%, 1.5% and 0.8% of a circular area having a radius of 3, 6, 9 and 12 m, respectively. Therefore, an individual within 6 m of a labeled plot, not having its core of roots within the irrigation area, and having the capacity of extending lateral roots 6 m or more, will have a $\leq 3.5\%$ probability that a lateral root will encounter the irrigation plot and subsequently label the plant. The probability decreases inversely proportional to the square of the lateral root length. In fact, on March 14th, the observed frequency of individu-

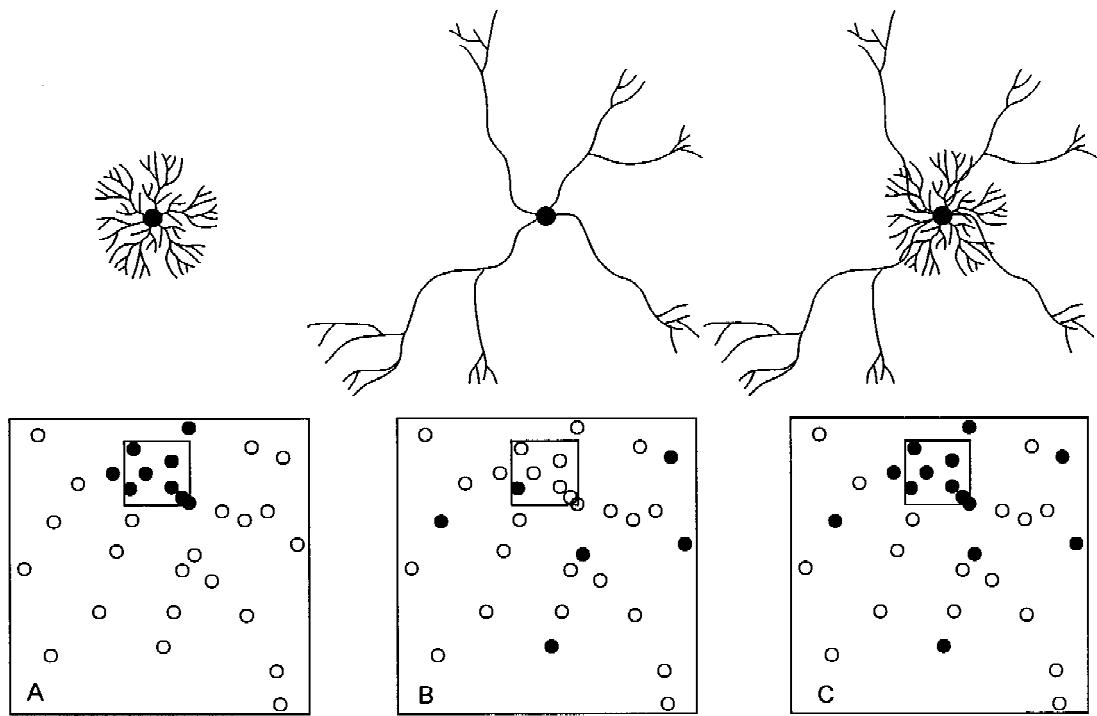


Figure 5. Possible rooting patterns for small trees and their expected labeling pattern. See text for explanation of different rooting patterns.

als 6 m or more away from the irrigation plot having deuterium label was greater than expected (observed 15%, expected $\leq 3.5\%$), suggesting that each individual probably has more than one of these long lateral straggler roots. This root structure is consistent with observations of high species diversity in root biomass per unit area in another site in the Amazonian basin having a forest with a similar structure as the one studied here (Restom, 1998). Core and lateral roots observed here could have a dual function in which lateral roots provide nutrients and core roots provide water. The importance of these lateral roots in terms of water and nutrient uptake relative to core roots, however, remains to be determined. Plants having a dual root system have been observed in other ecosystem particularly in arid regions (Dawson and Pate, 1996; Pate et al., 1995). In arid systems, however, lateral roots and taproots may have the additional purpose of acquiring different water sources (Dawson and Pate, 1996).

The results presented here also show that depth of water uptake by the trees in this particular study was shallow compared to a previous study in eastern Amazon (Moreira et al., 2000). Plant stem water within the irrigation plot had δD values which were

2%, 30% and 2% of the peak δD value of soil water when the peak was at the surface (3 days after irrigation), 0.3 m (15 days after irrigation) and 2 m deep (182 days after irrigation) respectively. Therefore, the highest water uptake occurred between the surface and at 2 m depth. Observations on the areas under the curves (Figure 2) when the soil water deuterium peak was 0.3 and 2 m deep (Figure 2) show that there was little loss of label between these two dates. Therefore, we can conclude that the bulk of water uptake occurred on the top half meter of the soil profile. The low labeled water uptake at the beginning of the experiment, when the δD value of soil water was highest and at the surface, may be due to a lag period between labeled water uptake and its appearance in the stem. Alternatively, the trees may not have been extracting water from the surface layer of the soil profile. The relatively wet dry-season observed in 1999 may explain the shallow water uptake during the beginning of the wet season (January 4, 2000) observed here. Labeled water uptake at deeper layers of the soil (below 2 m) either does not occur, or the label is diluted by water uptake from the shallower layers of the soil profile having unlabeled water. Fine root production in tropical forests is extremely dynamic (Sanford and

Cuevas, 1996), and root uptake at lower depths may be facultative, where fine roots grow at depth and begin absorbing water only when surface fine roots die down after surface soil water depletion. Further experiments are under way to determine if plants under imposed drought conditions can access water further down in the soil profile relative to that of control plants.

Finally, we note that our observations are only applicable to small trees and that quite possibly mature trees may have a much greater horizontal distribution of roots. In a Panamanian seasonal forest it was observed that trees with larger d.b.h. (≥ 0.5 m) were acquiring water from shallower layers of the soil than smaller individuals (Meinzer et al., 1999). This was interpreted as larger trees investing more carbon in widening their horizontal root distribution, whereas smaller trees may be investing more carbon in above ground biomass or increasing their depth of root penetration. This hypothesis will be tested using a larger area of irrigation, which will include larger trees.

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Section editor: B. E. Clothier