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Long range lateral root activity by neo-tropical savanna trees

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Abstract

The extent of water uptake by lateral roots of savanna trees in the Brazilian highlands was measured by irrigating two 2 by 2 m plots with deuterium-enriched water and assaying for the abundance of deuterium in stem water from trees inside and at several distances from the irrigation plots. Stem water of trees inside the irrigation plots was highly enriched compared to that of control trees, whereas stem water of trees just outside the plot was only slightly enriched compared with that from control trees. Therefore, bulk water uptake in the savanna trees studied occurred in a horizontally restricted area, indicating that their rooting structure was characterized by a dense cluster of short roots associated with the main trunk and a few meandering long range lateral roots. This root architecture was confirmed by extensive excavations of several species. The same deuterium labeling pattern was observed in an Amazonian tropical forest. The savanna ecosystem, however, differed from the tropical forest ecosystem by having a greater proportion of trees outside the irrigation plots having stem water with deuterium levels significantly above background. This leads us to the conclusion that savanna trees have more or longer lateral roots compared to tropical forest trees. The greater lateral root development in savanna trees may be an adaptation for more efficient nutrient absorption.

Introduction

Our understanding of root structure and function in neo-tropical savanna trees can be improved by studying their lateral root function in addition to their exploitation of deep soil moisture. The general thinking is that with an increase in aridity plants will tend to acquire water deeper in the soil profile (Canadell et al., 1996). Early work by Rawitscher (1948) for example, showed that in Brazilian savannas roots could extend as deep as 8 meters. Recent excavations in a wetter Amazonian seasonal tropical forest, however, have shown that roots of a seasonal tropical forest trees can be as deep as that observed in savanna trees (Jipp et al., 1998; Nepstad et al., 1994). Not much consideration has been given to the horizontal extent of soil resource exploitation by lateral roots as a function of the decrease in water availability. One large survey of the literature shows that shrubs tend to have shallower roots with a greater lateral spread in drier habitats (Schenk and Jackson, 2002). Indeed, trees of the savannas of Venezuela and Surinam have extended lateral roots at depths of 20 to 50 cm in addition to a deep vertical system (Sarmiento, 1984). It is not known whether these trends are a response to lower water availability or other edaphic factors associated with lower water availability. Schenk and Jackson (2002) hypothesized that the above trend is related to the extent of water infiltration in the soil water profile. However, there may be other edaphic factors associated with increasing aridity which may cause these

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particular root responses. For example: lower water availability can cause a build up of a lateritic barrier or calcareous layer a few decimeters below the soil surface (Brady and Weil, 2002). Dry habitats may have poor soil development or there might be a build up of elements that inhibit nutrient uptake (Brady and Weil, 2002). It is interesting to note that the previously reported trend of increasing lateral root spread with a decrease in precipitation only occurs in habitats having the bulk of their yearly precipitation in the summer (Schenk and Jackson, 2002). This observation indicates that the relationship between root architecture and climate may be more complex than a simple relationship between water availability and root structure. The interpretation of water and nutrient exploitation by lateral roots is complicated by the fact that most studies on lateral root development only determine their presence or absence. Their relative contribution to the plant's water and nutrient budget is usually unknown. Here we study the lateral water uptake patterns of trees in a neo-tropical savanna and compare them with those observed previously in a neo-tropical seasonal forest having a greater yearly precipitation and a less severe dry season (Sternberg et al., 2002). Specifically, we test the hypothesis that savanna trees have a wider area of bulk water uptake compared to tropical forest trees. We used a previously developed technique whereby a given area is irrigated with deuterated water and plants inside and in the neighboring area are assayed for the uptake of labeled water (Sternberg et al., 2002). This technique allows us to estimate the horizontal extent of water uptake by lateral roots and determine whether the bulk of water uptake in trees occurs within a limited area or not. The advantage of this method over root excavation is that it tests actual root function rather than merely their presence or absence.

Materials and methods

Site

The irrigation experiment was carried out in the Instituto Brasileiro de Geografia e Estatistica Ecological Reserve (Lat. 15° 56′ S, 47° 53′ W, RECOR) consisting of an open canopy savanna vegetation. This site is characterized by varying woody plant densities ranging from sparse (known as *campo sujo*) to small patches of dry forest (known as *cerradão*) (Eiten, 1984). The experiment was done in a *cerrado sensustrictu* characterized by a dense woody tree and shrub stand and a relatively flat terrain to avoid irrigation runoff. Rainy season at this site runs from October to April. During the months of June, July and August precipitation and relative humidity are very low. Although the soils at these sites consist of 72% clay they are well drained and deep (>3 m).

Root excavations

In August, 2000 surface roots of several species of small trees were excavated to a depth of approximately 30 cm and photographs of each root system were taken. These excavations were part of another study and done to better understand root structure for testing reverse sap flow in lateral roots with heat pulse probes. The following species were excavated: *Aspidosperma tomentosum* Mart. Arg., *Byrsonima crassa* Nied. *Blepharocalyx salicifolius* (H.B. & K.) Berg., *Caryocar brasiliense* Comb., *Dalbergia miscolobium* Benth., *Ouratea hexasperma* (St. Hil) Baill., *Qualea parviflora* Mart., *Roupala Montana* Aubl. *Schefflera macrocarpa* (C. & S.) Seem., *Sclerolobium paniculatum* Vog., *Stryphnodendron astringens* Mart., *Styrax ferrugineus* Ness et Mart.

Irrigation treatment

Two 2 by 2 m plots were delineated for irrigation with deuterated water. At each plot and surrounding area a total of 25 trees were selected, 5 of which were inside the irrigation plots. Trees located outside the plots ranged in distance from less than 1 m from the edge of the irrigation plot to approximately 12 m away. Each tree was labeled, their diameter at breast height (d.b.h.) measured, and classified into the following distance classes: 0–3, 3–6, 6–9, 9–12 m distance from the irrigation plot (Table 1). We did not sample the same number of individuals for each distance class. Because of the high species diversity at both sites, it was not possible to replicate treatments within a single species in a consistent and statistically viable way of testing for species effects.

Each treatment plot received 5 L of water (equivalent to 1.25 mm of precipitation) having 30% (volume) of 99.8% D_2O and 70% of water having background deuterium levels (about −20‰) during the wet season on February 17, 2003 when the soil profile was thoroughly saturated. Because this site had a dense layer of grass and herbaceous plants, we did not rake leaves before deuterated water application as done previously in a forest site (Sternberg et al., 2002). Irrigation with labeled water was followed by irrigation with 10 L/plot

Table 1. Species, d.b.h. and their respective distance class for 25 trees sampled in each replicate 2 × 2 meter irrigation plot

Species	d.b.h.(cm)	Distance	Species	d.b.h.(cm)	Distance
Emmotum nitens Miers	9.9	Inside	*Blepharocalyx salicifolius* H.B.& K.) O. Berg.	6.2	inside
Eremantus goyazensis.(Gard.) Sch .Bip.	7.4	Inside	*Emmotum nitens* Miers	3.9	inside
Kielmeyera coriaceae (Spr) Mart.	6.8	Inside	*Schefflera macrocarpa* C. & S.	4	inside
Qualea grandiflora Mart.	8.7	Inside	*Sclerolobium paniculatum* Vog.	2.5	inside
Sclerolobium paniculatum Vog.	4	Inside	*Sclerolobium paniculatum* Vog.	8.2	inside
Byrsonima crassa Nied.	7.5	0–3	*Caryocar brasiliense Camb.*	3	0–3
Eremantus goyazensis.(Gard.) Sch .Bip.	4.3	0–3	*Miconia ferruginata* DC.	8.3	0–3
Qualea parviflora Mart.	3.2	0–3	*Miconia ferruginata* DC.	3	0–3
Aspidosperma macrocarpon Mart.	6.3	3–6	*Qualea grandiflora* Mart.	2.2	0–3
Blepharocalyx salicifolius H.B.& K.) O. Berg.	11	3–6	*Sclerolobium paniculatum* Vog.	5.5	0–3
Blepharocalyx salicifolius H.B.& K.) O. Berg.	9.4	3–6	*Blepharocalyx salicifolius* H.B.& K.) O. Berg.	7.3	3–6
Blepharocalyx salicifolius H.B.& K.) O. Berg.	14.8	3–6	*Blepharocalyx salicifolius* H.B.& K.) O. Berg.	24	3–6
Dalbergia miscolobium Benth.	6	3–6	*Qualea grandiflora* Mart.	11.5	3–6
Dalbergia miscolobium Benth.	12.4	3–6	*Schefflera macrocarpa* C. & S.	11	3–6
Qualea grandiflora Mart.	11.3	3–6	*Caryocar brasiliense Camb.*	13.2	6–9
Qualea parviflora Mart.	3.8	3–6	*Erythroxylum suberosum* St. Hill	7.3	6–9
Schefflera macrocarpa C. & S.	10.4	3–6	*Byrsonima crassa* Nied.	5.7	9–12
Styrax ferrugineus Nees & Mart.	5.1	3–6	*Enterolobium ellipticum* Benth	9.3	9–12
Aspidosperma macrocarpon Mart.	4.6	6–9	*Miconia ferruginata* DC.	8.9	9–12
Sclerolobium paniculatum Vog.	3.8	6–9	*Ouratea hexasperma* (St.Hill) Baill.	6.8	9–12
Dalbergia miscolobium Benth.	18.3	9–12	*Qualea parviflora Mart.*	5.3	9–12
Enterolobium gummiferun Benth	9.3	9–12	*Schefflera macrocarpa* C. & S.	12.5	9–12
Qualea grandiflora Mart.	10.5	9–12	*Vochysia thyrsoidea* Pohl	14.2	9–12
Schefflera macrocarpa C. & S.	2.5	9–12	*Styrax ferrugineus* Nees & Mart.	9.7	9–12
Vochysia elliptica Mart.	6.1	9–12	*Vochysia elliptica* Mart.	5.5	9–12

of water (equivalent to 2.5 mm of precipitation) having background deuterium levels. The additional irrigation was done to 'push' the deuterium label further down in the soil profile and therefore prevent its loss by evaporation or equilibration with atmospheric vapor. The total amount of water applied during the wet season constituted about 0.32% of the total 2003 rainfall (1188 mm). Since this irrigation was done during the wet season and comprised a small proportion of the total yearly rainfall it should not have significantly affected plant water relations.

Sampling, water extraction and isotope analysis

Stem and soil water were collected 16 and 31 days after irrigation. We chose these sampling time intervals to be able to compare the results with those of a similar study in a tropical seasonal forest where samples were collected 15 days after irrigation (Sternberg et al., 2002). Stem samples were small, well suberized sections about 5 cm in length and 0.5 cm in diameter. Soil samples were collected with a soil auger at the surface, 25, 50, 75, 100, 125, 150 cm depth with two replicates in each plot per soil depth. Both soil and plant stems were sealed in small vacutainers, taken to the stable isotope laboratory at CENA or at the University of Miami and the water cryogenically distilled in a vacuum system (Moreira et al., 2000). Hydrogen isotope ratios were determined by reaction with zinc (Coleman et al., 1982). Hydrogen gas was analyzed either on a Finnigan Delta+ (CENA) or a Micromass Prism Isotope Ratio Mass Spectrometer (UM) with a precision of ±0.5‰. All values are reported here as δD values where:

$$\delta D(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 10^3 \quad (1)$$

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

Data analysis

We merged the isotope ratios of soil water from both plots and report the δD values as a single average for each depth, since there were no differences in the depth of peak hydrogen isotope ratios between both replicate plots. All statistical tests were carried out on the arc-sine transformation of the absolute D/H values of each sample. The mean δD values of stem water for each distance class were compared with that of the control group using a *t*-test (Sokal and Rohlf, 1995). Isotope ratios of stem water from individual plants were compared with the control population using the method of Sokal and Rohlf (1995) for comparing a single observation with a population. We compared the extent of lateral water uptake in this study with that observed in a similar previously published experiment conducted in a tropical seasonal forest (Sternberg et al., 2002). For this comparison we used forest and savanna results for the dates where maximum label was observed in individuals. This date was also characterized by having individuals inside the irrigation plots for both experiments with similar amount of label. After scoring each individual for the presence or absence of the tracer we used a logistic regression to test whether there were significant effects of vegetation type and distance on the probability of tracer uptake. The likelihood ratio test (-2LL) was used to test for these effects by comparing the full model with a nested null model (Rice, 1988).

Results

Observations of excavated root systems indicated that all species had on average 4 to 6 lateral roots some of which extended several meters from the main trunk of the tree (Figure 1).

The peak δD value of water from the savanna soil profile was observed at a depth of about 25 cm 16 days after irrigation and about 50 cm depth 31 days after irrigation (Figure 2). All of the trees inside the irrigation plots took up the deuterium label and showed sap water with significantly higher δD values compared with that of the control. These δD values ranged from +185‰ to +2753‰ 16 days after irrigation and +42‰ to +1342‰ 31 days after irrigation. The average δD values of stem water of the replicate plots were +1309‰ and +708‰ 16 days after irrigation and +473‰ and +431‰ 31 days after irrigation (Figure 3). There was a sharp drop in the average δD values for sap water for plants just outside the irrigation plot (0–3 m distance from irrigation plot, Figure 3). Although average δD values of sap water for plants at 0–3, 3–6, 6–9 or 9–12 m distance from the irrigation plot were low compared with those inside the irrigation plot, one treatment replicate had average δD of sap water significantly higher than the control for plants as far as 3–6 m away from the irrigation plot and another treatment plot had sap water with significantly higher average δD values compared to the average of control plants for plants up to 9–12 m away from the irrigation plot (Figure 3).

A comparison of the δD of sap water for single individuals relative to the control population indicated that all individuals within the irrigation plots were labeled by the deuterium application at both 16 and 31 days after label application (Figure 4). Sixteen days after irrigation 38%, 71%, 50% and 14% of the individuals were labeled at 0 to 3 m, 3 to 6 m, 6 to 9 m and 9 to 12 m away from the irrigation plot respectively. Thirty one days after irrigation 38%, 36%, 25% and 7% of the individuals were labeled at 0 to 3 m, 3 to 6 m, 6 to 9 m and 9 to 12 m away from the irrigation plot respectively (Figure 4). We did not observe any individuals that became labeled 31 days after irrigation that were not labeled 16 days after irrigation.

The fraction of labeled individuals declined sharply in both savanna (-2LL = 14.84, $P = 0.0001$) and forest (-2LL = 29.06, $P \ll 0.0001$) with increasing distance from the plot (Figure 5). However, this decline with distance was significantly more rapid in forest than in savanna (-2LL = 8.67, $P = 0.003$) such that there were more labeled individuals far from the irrigation plot in the savanna compared with that observed in the forest experiment (Figure 5).

Discussion

If all water uptake in trees only occurs within a relatively small area, then one would expect that stem water from trees inside the irrigation plots would have a high δD value and trees just outside would have virtually no label (Figure 6A). Further, few to none of the individuals at 0 to 3 m from the irrigation plots would be labeled, and individuals at greater distances would not be labeled at all by the deuterium application (Figure 6A). On the other hand if individuals had a relatively large area of bulk water uptake, one would expect that the δD value of stem water for individuals inside and those just outside (0–3 m) would

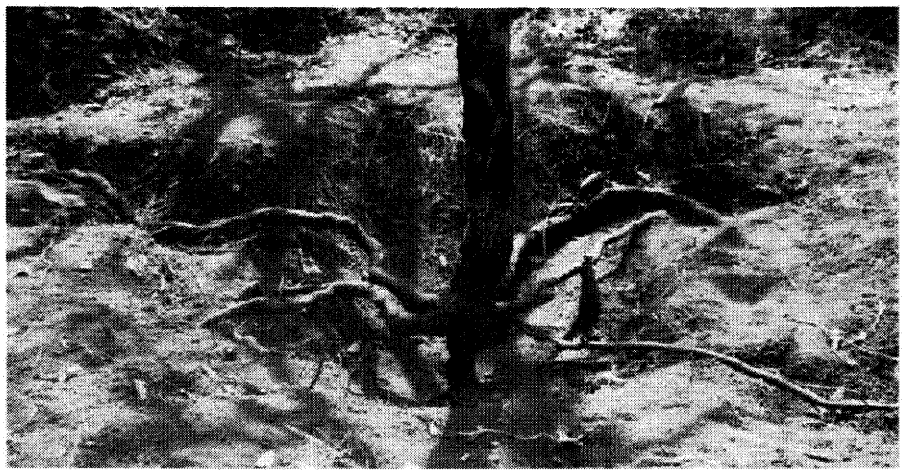

Figure 1. Photograph of typical root structure in *Byrsonima crassa* showing several lateral roots. Lateral roots shown here extended several meters distance from the main trunk. This root structure is typical of several species excavated at this site. Tap root and fine roots associated with the tap root not shown.

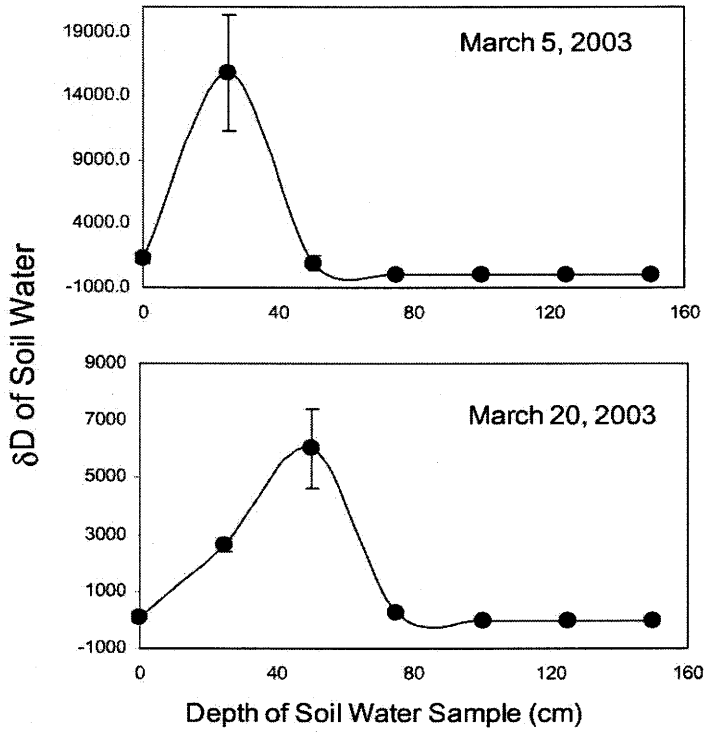

Figure 2. Average δD values of soil water (± Standard Error of the Mean, SEM) pooled from two irrigation treatments versus depth. The percolation of the applied deuterated water is shown 16 days (March 5, 2003) and 31 days (March 20, 2003) after irrigation of plots.

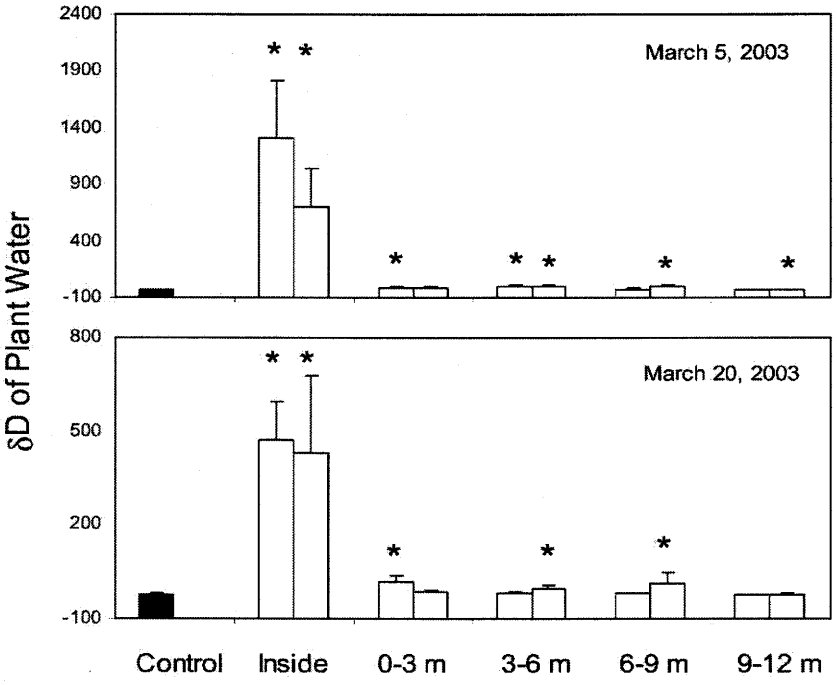

Figure 3. Average δD values ($\pm$ SEM) of plant stem water for control plants (black bars) and plants inside and several distance classes from the irrigation plots (white bars) for two dates. Star above each bar indicates a significant difference ($P \leq 0.05$) between the average for a particular distance class and control.

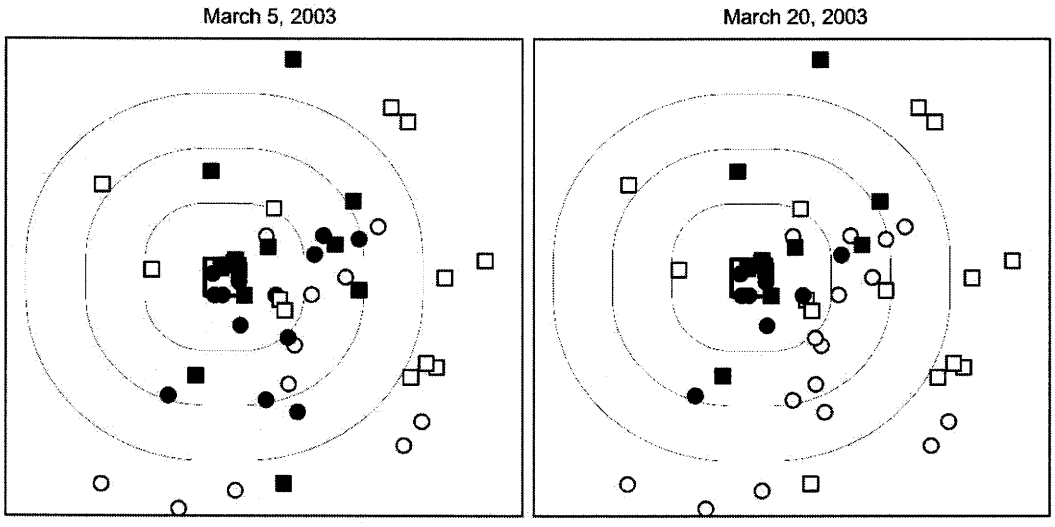

Figure 4. Mapping of plants inside and outside deuterium labeled plots for March 5 and 20, 2003 (each plant is represented by either a circle or a square symbol for each of the two treatment replicates). Dark symbols indicate plants having stem water with significantly higher δD values relative to those of control samples. Contour lines indicate 3, 6 and 9 m distance from the irrigation plot.

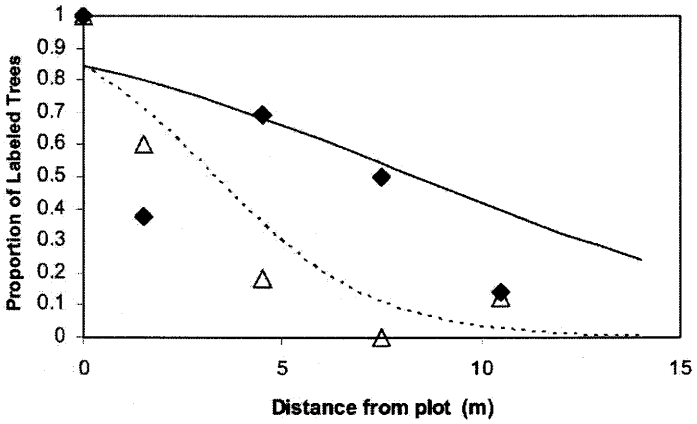

Figure 5. Percentage of plants at each distance class having sap water with significantly higher δD values than control plants for pooled replicates in the savanna site (black diamond, 16 days after irrigation) and the tropical forest site (white triangle, 15 days after irrigation). Also shown is the logistically fitted decay curve for savanna (solid line) and tropical forest (dashed line).

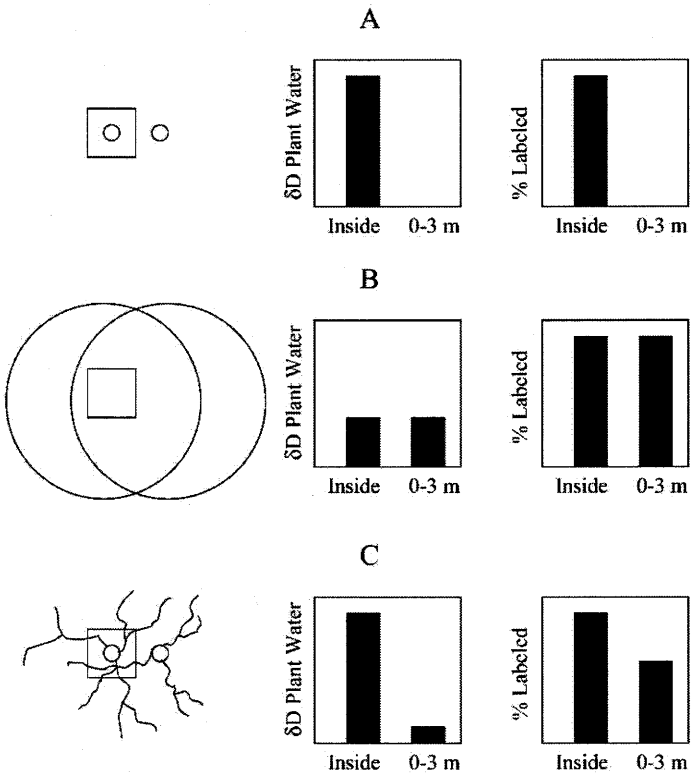

Figure 6. Hypothetical lateral root water uptake strategies (A, B, C), the expected relative average δD for plants inside and just outside (0–3 m) the irrigation plots and the expected frequency of labeled plants inside and just outside the irrigation plot for each water uptake strategy. Circles represent the area of bulk water uptake for each plant. Long range lateral roots in addition to area of bulk water uptake are only shown on the third scenario.

be approximately the same (Figure 6B). Likewise, an equal proportion of individuals both inside and just outside the irrigation plot, at 0 to 3 m distance, would be labeled by the deuterium application (Figure 6B). A third possibility is that trees would have the bulk of water uptake from a relatively small area and a small amount of water uptake at greater distances from their main stem. The root architecture for this particular scenario would be one where there is a denser core of roots close to the main stem and a few long range meandering roots that take up water quite far from the main stem (Figure 6C, see also Figure 5 in Sternberg et al., 2002). The latter root architecture was confirmed for our study site by extensive root excavations showing a few long range lateral roots extending from the base of the main stem (Figure 1). We note that this particular root architecture does not necessarily require a specific growth pattern since the production of root volume with equal intensity, regardless of the distance from the main trunk of the parent tree, will result in a rapid decrease in root density proportional to the square of the distance from the main trunk.

The observed root architecture from the excavations was consistent with the water uptake pattern observed here. Qualitatively savanna trees had a water uptake pattern similar to Amazonian forest trees when examined according the above scheme. Both forest and savanna trees just outside the irrigation plots had sap water with very low deuterium levels compared with those inside the irrigation plot (Figures 3 and 4 in Sternberg et al., 2002). Therefore, the water uptake scenario shown in Figure 6B is unlikely. Although the amount of label in the stem water for individuals just outside the irrigation plot was low compared to those inside the irrigation plot, there were some individuals several meters away from the irrigation plot which were labeled by the deuterated water treatment (Figure 4 and 3 in Sternberg et al., 2002). Therefore, water uptake by roots of savanna trees more closely resembles the third scenario (Figure 6C) as it was previously observed in a tropical forest. Savanna trees, like forest trees, have the bulk of water uptake within a relatively small area and a minor component of water uptake from long range lateral roots.

Quantitatively savanna trees differed from forest trees in the number of individuals at greater distance from the irrigation plot that were labeled. Average δD values of sap water from savanna trees as far as 9 to 12 m from the irrigation plot were significantly greater than that of the control (Figure 3) whereas in the forest significant amounts of label were only found as far as 3 to 6 m from the site of irrigation (Figure 4 in Sternberg et al., 2002). A significantly greater proportion of savanna trees 3 to 6 and 6 to 9 m away from the irrigation plot were labeled compared with forest trees (Figure 5). Although savanna and forest trees may have a similar lateral extent of bulk water uptake, their label uptake pattern suggests that they have a greater number of and/or longer lateral roots meandering off their main stem. This is consistent with the much greater root/shoot ratios of savanna species compared with those of forest species (Castro and Kauffman, 1988; Hoffman and Franco, 2003). One possibility is that the higher peak deuterium concentration in the savanna soil water ($\sim$+16,000‰) compared with that of the forest site ($\sim$+3,500‰) increases the sensitivity of the assay and allows us to detect smaller amounts of water uptake further from the irrigation plot. We note, however, that the average δD values of stem water for plants inside the irrigation plot are similar for the savanna (+1,309 and +708‰) and forest trees (+1,443 and 883‰) at the dates being compared. Therefore the sensitivity of the test for lateral water uptake by plants at both of these sites is probably similar.

The general thinking about savanna trees is that water uptake occurs at a greater depth compared with that of tropical forest trees. But recent studies in seasonal tropical forest indicate that roots of both forest and savanna trees can penetrate to depths below 8 m (Jipp et al., 1998; Nepstad et al., 1994). Further, a large survey of over 1300 records of root systems in habitats with $\leq$ 1000 mm of annual precipitation indicates that shrubs in drier habitats have wider root architecture with a low depth of soil penetration (Schenk and Jackson, 2002). Greater lateral root networks in savanna trees maybe adaptive to three characteristics of the savanna habitat: high wind, low water and nutrients.

According to a biomechanical model, superficial lateral roots are more efficient than deep vertical roots in anchoring plants with large above ground sizes (Ennos, 1993). Tropical forest trees, however, are much taller than savanna trees and blow-down in the Amazonian forests is quite common (Nelson, 1994). There are no substantial differences in wind velocities between these two sites and therefore larger lateral roots in savanna plants as an anchoring adaptation is unlikely.

Tropical savannas can have as much annual precipitation as tropical forests, but the major climatic difference between these two ecosystems is the dry season severity (Nix, 1983). Savannas have a longer

and dryer dry season compared to tropical forests. However the severity of the dry season at our study site is such that the water potential of soils 1m deep is rarely below −1.0 MPa, even though the water potential in the top 5 cm of the soil profile can fall as low as −2.0 to −3.0 MPa (Franco, 2002). Therefore water availability does not pose a problem for vertical roots of savanna trees at our site. Indeed, previous studies indicate that there is no substantial decrease in transpiration during the dry season (Meinzer et al., 1999). Given the low water potentials near the soil surface, it seems unlikely that plants would develop a greater root spread to exploit soil water at the top 10 cm of soil. Another possible explanation for the extensive lateral root development in savanna trees is that they utilize surface water redistributed to the surface by hydraulic lift in deep rooted plants (Moreira et al., 2003; Scholz et al., 2002). However, studies using isotopically labeled water indicate that hydraulic lift probably does not provide sufficient water at the soil surface layers to directly affect water relations (Moreira et al., 2003). The preceding suggests that the greater root spread in savanna trees is probably not functioning as an adaptation for more efficient water uptake.

Tropical savannas in Brazil are known to have a phosphorus deficit as do tropical forests (Haridasan, 2000; Lopes and Cox, 1977; Vitousek 1984). In addition aluminum toxicity inhibits substantial nutrient uptake in Brazilian savannas (Reatto et al., 1998). Like several other ecosystems, savannas have a gradient in nutrients with surface layers of the soil profile showing a greater nutrient concentration compared to deeper layers of the soil profile (Jobbagy and Jackson, 2001). Because the dry season in savannas may cause a more severe drying of the top layers of the soil profile compared to that of tropical forests, nutrients at the top layers of the soil profile may be relatively less available to savanna trees compared to tropical forest trees. Therefore the clearest edaphic contrast between tropical forests and savanna is the availability of nutrients at the top layers of the soil profile and we hypothesize that the more extensive lateral root development in tropical savannas may be an adaptation to better exploit the nutrients at the top layer of the soil profile.

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