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Carbon Inputs and Water Uptake in Deep Soils of an Eastern Amazon Forest

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Abstract: Rooting depth affects soil profiles of water uptake and carbon inputs. Here we explore the importance of deep roots in a mature tropical forest of eastern Amazonia, where a throughfall exclusion experiment was conducted to test the resilience of the forest to experimentally induced drought. We hypothesized that soil water depletion occurred below the depth previously measured by sensors in 11-m-deep soil pits and that only a small root biomass is necessary to affect water uptake and the isotopic signature of soil CO_2. A noninvasive electrical profiling method demonstrated greater depletion of soil water in the 11–18 m depth increment in the exclusion plot compared with the control plot by the end of the 3rd year of the experiment. A fine root biomass of only 0.1 g/cm^3 measured at 3–6 m was sufficient for soil water drawdown and for imparting an isotopic signature of modern soil $^{14}CO_2$ in both plots. A soil $^{13}CO_2$ profile indicated drought stress in the exclusion plot. Fine root inputs of organic C to deep soils are small with respect to the carbon dynamics of the forest, but the deep rooting habit clearly affects the ecosystem water balance and profiles of soil CO_2. FOR. SCI. 57(1):51–58.

Keywords: CO_2, roots, soil organic matter, soil resistivity, soil water

THE CYCLES OF CARBON, water, and energy are inextricably linked in terrestrial ecosystems through the process of photosynthesis. These linkages affect soil processes through the activity of roots, which utilize carbon fixed by the plant to acquire nutrients and water from the soil. Where roots are present, organic carbon is input to the soil through root exudation, mycorrhizal associations, and death of root tissues, and CO_2 is generated from root respiration and microbial decomposition of dead roots. Downward transport of dissolved organic carbon may also be important in some soils, but the depth to which plants extract water from the soil clearly establishes the minimum depth to which organic and inorganic carbon enter the soil.

Deep roots are common in water-limited ecosystems (Rawitscher 1948, Schenk and Jackson 2002). Although Amazon rainforests are sometimes erroneously assumed to be continuously wet, deep roots are common in the eastern Amazon, where seasonal drought requires that plants utilize soil water that is drawn down during the dry season and recharged during the wet season (Nepstad et al. 1994, Jipp et al. 1998, Brando et al. 2008). These studies have demonstrated that water extraction occurs to as much as 11 m depth. Deep roots of some species have been shown to redistribute water to more shallow depths by hydraulic lift (Oliveira et al. 2005).

The contribution of deep roots to carbon cycling processes is complex. Radiocarbon studies have demonstrated that deep soil organic matter is dominated by very old carbon that has been isolated from exchange with the atmosphere for thousands of years (Trumbore et al. 1995). In contrast, the CO_2 within the deep soil profile contains an isotopic signature that is higher than the modern atmosphere, indicating that root respiration and decomposition of organic matter that had been fixed within the last few decades contributes the majority of deep soil CO_2 (Trumbore et al. 1995, 2006).

Here we explore the importance of deep roots in a mature tropical forest of eastern Amazonia, where a throughfall exclusion experiment was conducted to test the resilience of the forest to experimentally induced drought. Previous studies demonstrated that soil water was depleted in the exclusion plot to at least 11 m, which was the deepest time domain resistivity (TDR) sensor at the lowest possible depth of the soil pits dug for that study (Brando et al. 2008). In the present study, we used a noninvasive electrical profiling method to measure soil water content to depths >20 m in control and exclusion plots. We hypothesized that this technology would demonstrate that soil water depletion occurred below 11 m depth in the experimental plot.

Previous studies also demonstrated that the exclusion treatment did not significantly affect rates of CO_2 efflux from the soil surface or its ^{14}C signature, but that the ^{13}C signature was affected by the drought treatment (Brando et al. 2008). Here we present profiles of $^{14}CO_2$ and $^{13}CO_2$ to 11 m depth to examine effects of throughfall exclusion on deep carbon processes. Measures of fine root biomass to 6 m depth are also presented to demonstrate the relation between root biomass and observed differences in carbon

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isotopes and water uptake. Previous studies have shown that the fine root biomass usually declines exponentially with soil depth (Nepstad et al. 1994, Schenk and Jackson 2002), which means root biomass is generally low in deep soils. We hypothesized that only a small root biomass in deep soil is capable of significant water uptake and of imparting an isotopic signature of soil CO_2.

Materials and Methods

Site Description

The experiment was carried out in the Tapajós National Forest, Pará, Brazil (2.8978°S, 54.9528°W). Emergent trees extend up to 55 m in height, with a continuous canopy varying in height from 18 to 40 m. Annual precipitation ranges from 1,700 to 3,000 mm and averages approximately 2,000 mm, with a 6-month dry season (July–December) when rainfall rarely exceeds 100 mm/month. Annual precipitation was 2,697, 1,913, 1,942, 1,692, and 2,345 mm in 2000–2004, respectively. Mean annual temperature is 25°C (minimum 22°C, maximum 28°C). The soil is deeply weathered Haplustox. The depth to water table at a similar site 12 km away was ~100 m, which means that the stocks of soil water available to trees is recharged only by rainfall.

Experimental Design

The throughfall exclusion experiment consisted of two structurally and floristically similar 1-ha plots: an "exclusion plot" (treatment) and a "control plot." We encountered 182 and 203 species represented by individuals with dbh (1.3 m) of at least 10 cm for trees and 5 cm for lianas in the treatment and control plots, respectively (Nepstad et al. 2002). Aboveground biomass of trees >10 cm dbh and lianas >5 cm basal diameter at the beginning of the experiment was 291 and 305 Mg ha^{-1} in the treatment and control plots, respectively. The basal area of trees >10 cm dbh was 32.5 and 30.9 m^2 ha^{-1} in treatment and control plots, respectively.

In the exclusion plot, 5,660 plastic panels, each 3 × 0.5 m, diverted throughfall into plastic-lined, wooden gutters, which carried the water into a plastic-lined trench around the plot perimeter, which then flowed to a deeper drainage ditch extending 220 m away from the plot and into a small valley. This system of panels and drains diverted approximately 34–40% of annual incoming precipitation (70% of throughfall) during the 6-month wet seasons (December–May) from 2000 through 2004. For consistency, the control plot had a similar trench around its perimeter, but no water was diverted. The panels were removed during the dry season to reduce their influence on the forest floor through shading and heating. While they were in place, the panels were flipped on their sides every 2–3 days to transfer accumulated litter onto the forest floor beneath. More complete details of the experimental design have been published elsewhere (Nepstad et al. 2002, 2007, Davidson et al. 2004, 2008, Brando et al. 2008). As with other large-scale, unreplicated experiments (Hurlbert 1984), the throughfall exclusion treatment effect was determined by evaluating the divergence of each response variable between the treatment and control plots over time.

Because of methodological and logistical constraints, it was not possible to measure root biomass, soil CO_2 profiles, volumetric soil water content, and soil electrical properties to the same depths or on the same dates. Some of these measurements were originally intended for other research questions, but we assemble them here to address the common theme of the importance of deep soil processes that are related to the carbon cycle.

Volumetric Water Content

Volumetric Water Content (VWC) was quantified using TDR (Topp et al. 1980) in five soil pits within each plot. The TDR measurements were made monthly from 2000 to 2005. For the top 30 cm, a pair of 30-cm-long probes was inserted vertically from the surface at a location adjacent to each pit. For 0.5 m, 1 m, and each subsequent meter to 11 m depth, a pair of probes was inserted horizontally into opposite walls of each soil pit. Each probe was installed at the end of a 1.5-m auger hole drilled horizontally into the wall of the pit (the rods pushed into the intact soil) to avoid pit wall effects on soil moisture; the holes were then back-filled with soil. The TDR readings were converted to VWC using the calibration of Jipp et al. (1998) derived on similar Oxisols.

Two-Dimensional Resistivity Profiling

Measuring electrical resistivity of the soil is a nondestructive method to study several spatially and temporally varying soil physical properties, including structure, water content, and fluid composition. It has been applied to groundwater exploration, landfill and solute transfer delineation, agronomy, hydrology, soil science, and ecology (Samouëlian et al. 2005, Ferreira et al. 2007, Garcia-Montiel et al. 2008). Measurements of soil resistivity consist of injecting a continuous current into the ground through two current electrodes (C1 and C2) and measuring the resulting voltage difference in two other potential electrodes (P1 and P2). Voltage and current measurements are obtained from an array of electrodes placed on the ground surface along a line of measure (Seaton and Burbey 2002). The assignment of currents and potential electrodes at each point measurement is determined by a specific electrode configuration moving along the measured line. An apparent resistivity value is then calculated by knowing the intensity of the injected current, the difference in voltage, and the geometric positions of the electrodes C1, C2, P1, and P2, determined by the array of the electrodes. The true resistivity values are then determined with an inversion of the apparent resistivity values using computerized inversion programs. The resultant product is a two-dimensional (2-D) Earth model of resistivity distribution in the subsurface environment (Loke and Barker 1996).

Field resistivity measures were conducted with a commercially available earth resistivity meter, the SuperSting R1/IP single-channel Earth Resistivity meter connected to a

Swift Dual Mode automatic multielectrode system (Advanced Geosciences, Inc., Austin, TX). For each 100 × 100-m study plot, a 56-electrode cable was laid out along a 275-m transect, with the study plot (control or throughfall exclusion treatment plot) roughly within the center of the transect. The electrode spacing along the transects was 5 m, resulting in a maximum soil resistivity profile depth of 42 m. Individual electrodes were secured on the surface by stainless steel stakes inserted in the soil and equipped with a spring contact to hold the electrode.

The resistivity meter automatically and systematically selects pairs of current and potential electrodes along the line of measurement to measure resistivity at varying vertical and horizontal positions along a 2-D profile, using a Wenner sampling array (Sharma 1997, Seaton and Burbey 2002). Data were accepted when the difference in duplicate resistivity measures taken at one data collection point was less than 5%. Field measurements of apparent resistivity were inverted with the EarthImager 2D software developed by Advanced Geosciences, Inc. To estimate resistivity for depth increments along the horizontal transects, we used the nonconstrained Delaunay triangulation model provided in the triangulated irregular network tool of the GIS software, IDRISI Kilimanjaro version 14-02 (Eastman 2003) for data interpolation. The interpolated resistivity profile raster grids were then imported into Arc-GIS 9.3 for visual display and for data extraction. Resistivity values were extracted for specific depths (0.1, 0.3, 0.5, 0.7, 0.9, and 1.5 m and then 1-m intervals throughout the measurement profile at each electrode position. Means were calculated for each soil depth across the 80-m horizontal portions of the transects that fell within the study plots, excluding a 10-m buffer at each end of the plot.

To estimate VWC from the resistivity measurements, a calibration equation was developed. Each transect of resistivity measurements passed by three of the soil pits within each plot. The measured resistivity values were extracted from the 2-D profiles for the 10-m-wide area adjacent to each soil pit and for each TDR probe depth at each measurement date. Regression analysis was used to relate VWC measured by TDR measurements to resistivity values measured at the same locations and depths for the same period. The calibration equation was then applied to mean resistivity measurements for each soil depth of each study plot at each date to estimate mean VWC by depth, date, and plot.

Fine Root Biomass

Live fine root biomass (0–2 mm diameter) was determined based on 20 auger borings to 6-m depth in each plot, with 1.5-kg soil samples collected at 0–0.1, 0.5, and 1 m and at 1-m intervals to 6-m depth. Roots were separated from the soil using a combination of sieving of the soil in suspension through a 0.6-mm nylon mesh and visual inspection of the soil slurry after sieving. The mass of roots was estimated per gram of dry soil, and the mass per unit volume of soil was estimated using measures of bulk density.

CO$_2$ Gases and Isotope Signatures

We obtained CO$_2$ for isotopic analyses by withdrawing 60 ml of air from gas tubes installed at depths from 1 to 11 m into the wall of each soil pit, following the method of Davidson and Trumbore (1995). The syringe air was used to flush and fill serum vials (125 ml) for storage and transfer of samples to the University of São Paulo at Piracicaba and the University of California at Irvine for ^{14}C analyses (Trumbore et al. 2006). For sampling of soil air above 1-m depth, we used pre-evacuated 500-ml steel containers attached directly to the steel sampling tubes.

The CO$_2$ was purified from air cryogenically. An aliquot was stored for measurement of ^{13}C and 2 ml of purified CO$_2$ was sealed into a tube with reagents (zinc and titanium hydride) and a catalyst for reduction of CO$_2$ to graphite for accelerator mass spectrometry measurement (Xu et al. 2007).

Results

Two-dimensional resistivity profiles show greater resistivity near the soil surface, indicating drier soils at surface horizons (Fig. 1). A clear pattern of greater resistivity is also apparent (more yellow-red colors) to approximately 15–20 m depth within the 100-m-wide exclusion plot.

Calibration of resistivity with TDR (Fig. 2) follows the same curvilinear pattern reported by Garcia-Monteil et al. (2008). The calibration used data from 0.5–11 m depths from four measurement dates in both control and treatment plots. There was no bias in the residuals of the calibration equation that would indicate a need for separate calibrations by treatment or soil depth, although we found it necessary to exclude data from the 0.1–0.3 m depths, because they did not follow the same pattern. The regression equation tends to underestimate VWC at these shallow depths, but we do not have sufficient data to derive a separate calibration equation that would improve the fit, and the resistivity data at these shallow depths may not be reliable. The spacing of electrodes is a compromise between putting them far enough apart to be able to estimate deep soil resistivity but also close enough together to resolved differences at the submeter scale. The 5-m spacing used in this study enabled deep profiling of electrical properties but probably resulted in less reliable estimates of resistivity of the top 30 cm.

Soil water contents to 20 m depth estimated by resistivity are shown for six dates in Fig 3. We cut off the analysis of VWC at 20 m depth because there were no consistent differences in raw resistivity values between control and exclusion plots below this depth. The profiles of water content in control and exclusion plots were similar in March 2001, early in the experiment, but diverged at 6–14 m depth by December 2001. The differences between plots in the top 11 m of the soil profile were greatest in April and July 2002 (Fig. 3; Table 1), which was the third exclusion period and approximately when significant tree mortality started to be observed (Nepstad et al. 2007, Brando et al. 2008). The differences in water content of the top 11 m between drought treatment and control plots were somewhat less in December 2002 and December 2003. December is the end
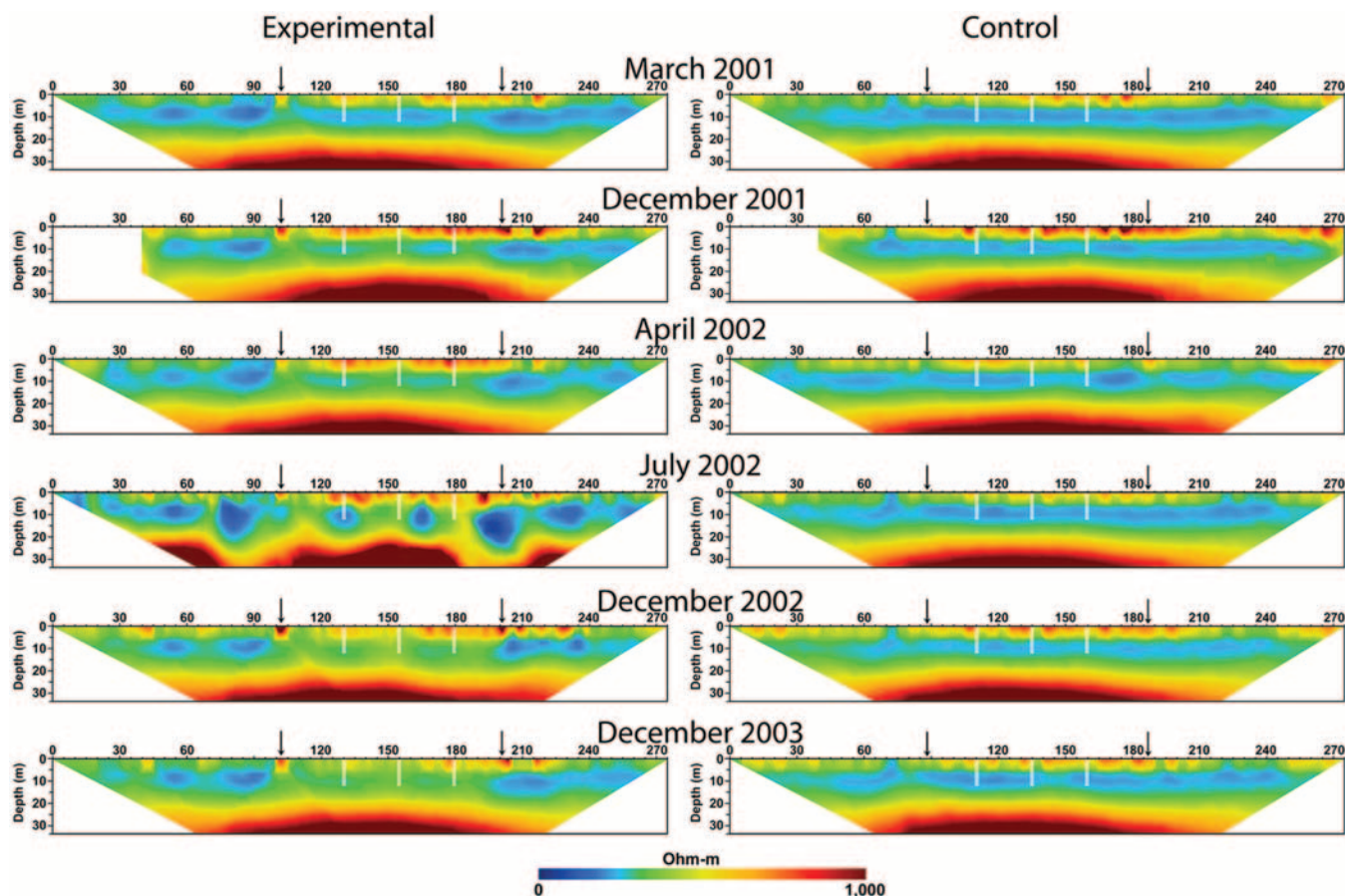
Figure 1. Resistivity profiles along 275-m transects that include the exclusion and control plots for six dates. Arrows indicate edges of the 100-m plots. White bars indicate the location and depth of three soil pits along each transect. The shading shows values of resistivity in units of ohm-m. Blues indicate low resistivity and high water content; reds indicate high resistivity and low water content.
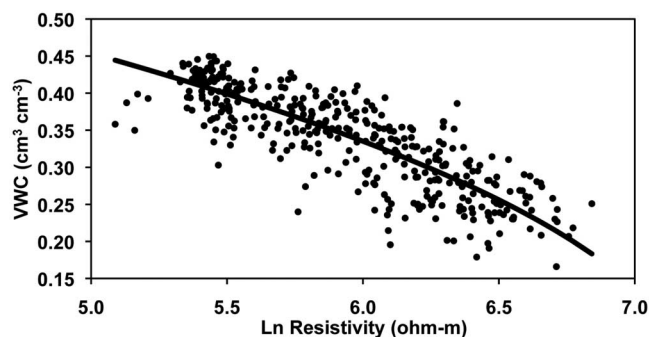

Figure 2. Calibration of resistivity measurements to estimate VWC, using time domain reflectometry measurements in soil pits. The calibration curve is VWC = $\sqrt{[(-0.0935 \times LnR) + 0.6733]}$, where LnR is the natural logarithm of resistivity. R^2 = 0.74; $P < 0.0001$.

of the dry season, when less contrast between plots is expected owing to naturally dry conditions in control plots resulting from plant uptake of water throughout the dry season. However, differences between plots in deep soil water (11–18 m) did not develop until about December 2002, indicating that trees in the drought experiment plot were then accessing very deep soil water after 3 years of experimental throughfall exclusion (Fig. 3; Table 1), perhaps because further water extraction from surface soil in

the exclusion plot was limited. Overall, from December 2001 onward, the exclusion plot had 124–376 mm less water present in the top 18 m of the soil profile (Table 1).

The soil CO_2 concentrations and their isotopic signatures are shown in Fig 4. There were no differences between treatments in CO_2 concentrations or $^{14}CO_2$, indicating that throughfall exclusion did not affect the relative age of carbon substrates being respired. In contrast to ^{14}C, there were differences in $^{13}CO_2$ throughout the soil profile but especially in the top 1 m. Hence, the throughfall exclusion treatment provoked water stress that affected the ^{13}C signature of the photosynthate, including the carbon that was allocated belowground for root respiration. The effect is apparent as deep as we could measure using tubes inserted into soil pit walls to 11 m depth. Both the ^{14}C and ^{13}C isotopic signatures indicate that modern root carbon dominated the soil CO_2 concentrations at all depths and that drought stress had altered the $^{13}CO_2$ signature of root respiration.

Fine root biomass data are presented in Fig. 5 for treatment and control plots to 6 m depth. There are no statistically significant treatment effects, although these measurements were made only early in the experiment. Fine root biomass dropped exponentially from the top to approximately 3 m depth and then was relatively constant from 3 to 6 m depth.
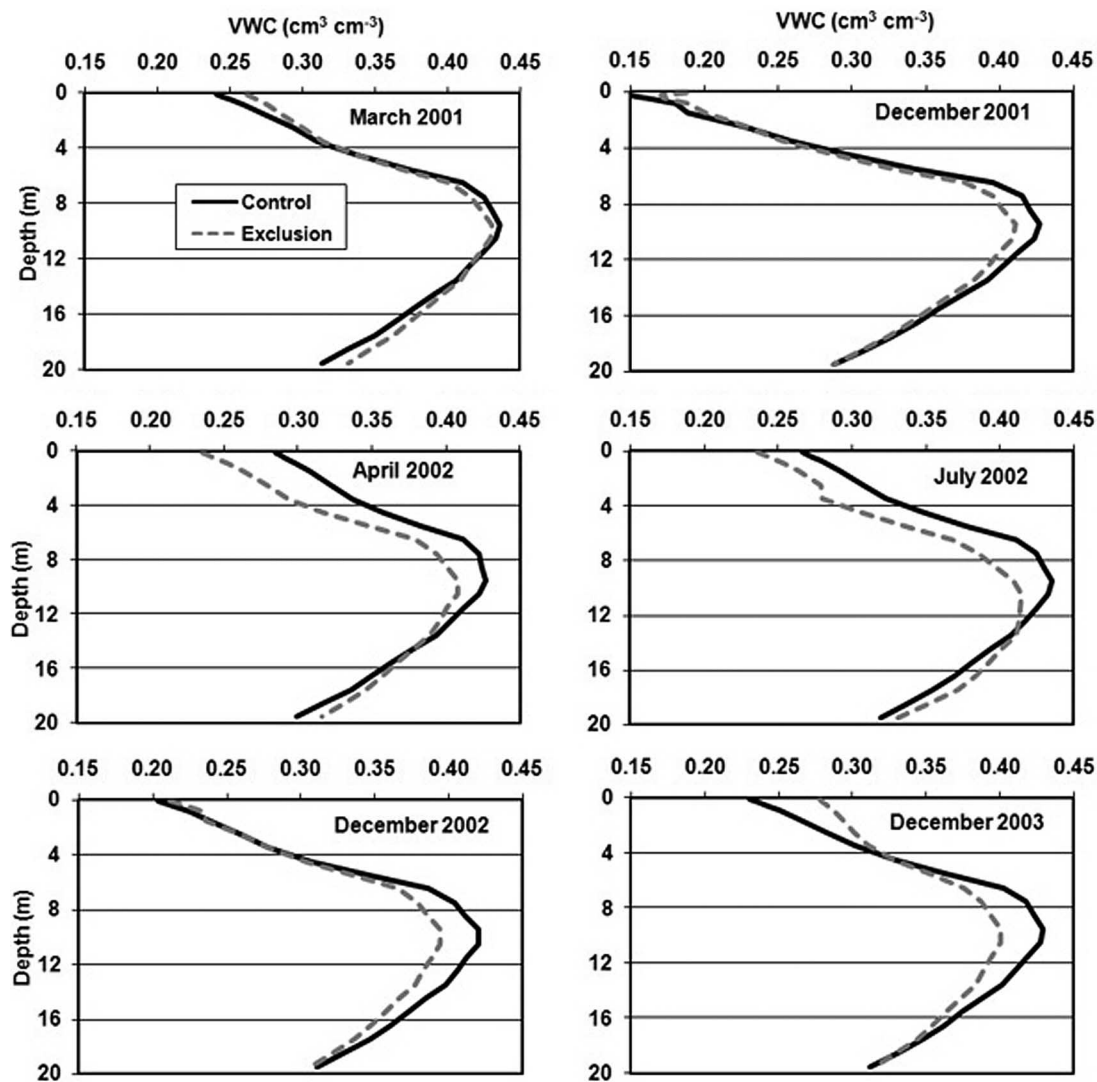
Figure 3. Depth profiles of estimates of VWC in control and exclusion plots based on the resistivity data shown in Fig. 1 and the calibration shown in Fig. 2.

Table 1. Soil water storage in control and throughfall exclusion plots and their difference by soil depth increment and date, estimated by soil resistivity

	Soil water storage (mm)											
	0–2 m			2–11 m			11–18 m			0–18 m		
Date	Cont.	Excl.	Diff.	Cont.	Excl.	Diff.	Cont.	Excl.	Diff.	Cont.	Excl.	Diff.
Mar. 2001	522	555	−32	3,447	3,422	25	2,725	2,765	−40	6,695	6,742	−47
Dec. 2001	351	381	−30	3,203	3,091	113	2,610	2,558	51	6,164	6,030	134
Apr. 2002	598	506	92	3,500	3,221	279	2,635	2,631	4	6,734	6,358	376
July 2002	566	508	58	3,488	3,175	313	2,746	2,785	−39	6,800	6,468	332
Dec. 02	452	458	−6	3,228	3,091	137	2,676	2,552	124	6,357	6,102	255
Dec. 03	504	574	−70	3,375	3,247	128	2,701	2,601	101	6,580	6,421	159

Cont., control; Excl., throughfall exclusion; Diff., difference.

Discussion

Deep Soil Water Uptake

The first hypothesis was affirmed: that more deep soil water depletion (below 11 m depth) occurred in the exclusion plot compared with that in the control plot. Active water uptake by deep roots to approximately 18 m depth can be inferred from the resistivity data (Fig. 3). Drainage alone would not result in soil drying to below field capacity (i.e., the water content held by the soil against the force of gravity), whereas root uptake of deep soil water that exceeds recharge from above can cause soils to become drier. Although there
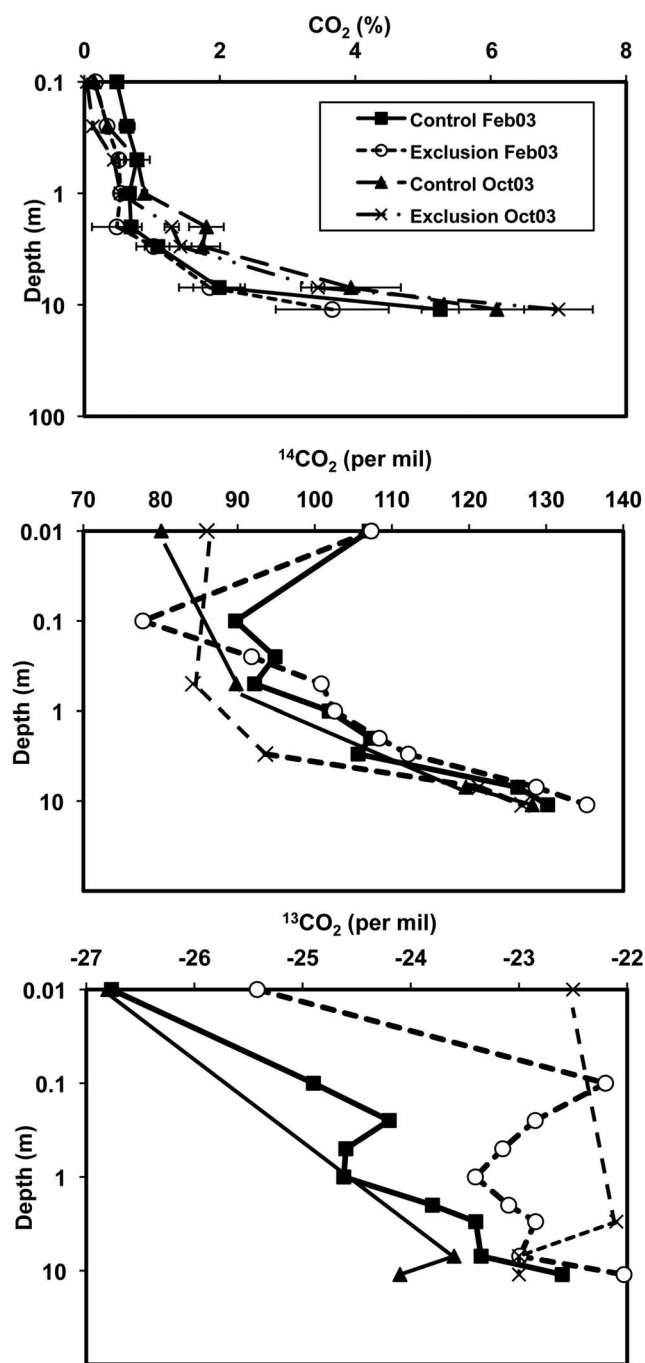
Figure 5. Live fine root (<2 mm) biomass in August 2000.

Figure 4. Profiles of soil CO_2 concentrations and isotopic composition.

probably were episodes when soil water content was above field capacity and was draining to lower horizons, we assume that resistivity measurements made between precipitation events measured water contents at or below field capacity and that differences between seasons and between exclusion and control plots reflect plant uptake that exceeded recharge.

The estimates of differences in soil water content derived from the resistivity measurements compare favorably with those reported for TDR measurements. Brando et al. (2008) estimated that the exclusion plot had 97 and 272 mm less water than the control plot in the 0–2 and 2–11 m depth intervals, respectively, after three periods of throughfall
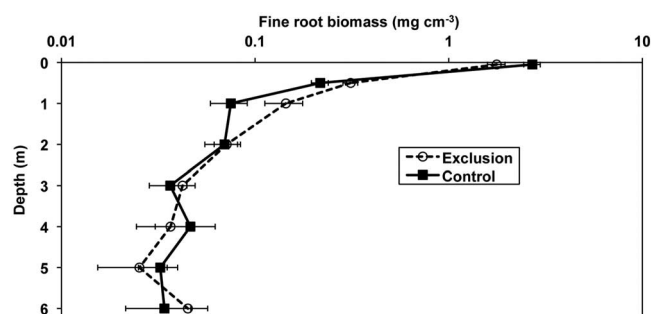
exclusion in 2002. For the same soil depth intervals and date, the resistivity-based estimates are 58 and 313 mm lower in the exclusion plot. Resistivity estimates may be less reliable near the surface with the electrode spacing that we used, but the agreement within 10% for the 2–11 m depth interval is remarkable.

Resistivity measurements permit measurement of this effect at depths that would be very difficult to access with digging or auguring. Although the TDR estimates are limited to access by the depth of the soil pits, the resistivity imaging allowed us to estimate differences in soil water content to 18 m and could have detected changes at lower depths if they had occurred. Furthermore, the resistivity-based estimates are averages that include spatial variability along an 80-m transect across each study plot (excluding a 10-m edge at each end of the 100-m plots), whereas the TDR data are from only five fixed soil pits.

The quantitative estimates of water contents below 11 m depth must be interpreted with some caution, however, because we cannot confirm that the calibration equation (Fig. 2) is valid below the depth of TDR measurements. Although the calibration equation was robust for all depths from 0.5 to 11 m, unknown changes in soil texture or mineralogy below 11 m depth could affect the relationship between resistivity and water content. Declining estimated VWC below 10 m (Fig. 3) depth probably reflects higher bulk density and lower porosity at these depths. Estimates of VWC below 11 m depth derived from resistivity profiling, whereas clearly demonstrating increasing qualitative differences between treatment plots over time, provide only approximate quantitative estimates of water volumes.

Deep Roots and Soil Carbon

The second hypothesis was also supported: that only a small root biomass in deep soil is necessary for significant water uptake and to affect the isotopic signature of soil CO_2. Root biomass values as low as 0.1 g/cm^3 at 3 m depth and lower were able to draw down stored soil water stocks and to impart an isotopic signal to soil CO_2 that is characteristic of modern carbon and, in the case of the experimental plot, characteristic of drought stress. Indeed, the drought treatment could be detected as less depleted $^{13}CO_2$ as deeply as we sampled gases, which was 11 m. This belowground response is consistent with measurements of the top-of-canopy foliar ^{13}C, which ranged from an average of −32/mil at the beginning of the experiment to −28/mil in 2003 in the

exclusion plot, whereas no change over time was detected in the control plot (Ehleringer et al. 2004). The soil $^{13}CO_2$ was about 4–5/mil heavier than foliar measurements, which is consistent with a 4.4/mil fractionation during diffusion within the soil (Cerling et al. 1991).

In contrast to the $^{13}CO_2$ effect, no effect of throughfall exclusion was observed for profiles of soil $^{14}CO_2$. The mean age of fine roots has been estimated to be at least 4 years (Trumbore et al. 2006), which means that a significant change in $^{14}CO_2$ derived from root decomposition would not necessarily be expected after only a few years of experimental throughfall exclusion. Although a treatment effect was not observed, the soil $^{14}CO_2$ profiles (Fig. 4) demonstrate that modern carbon inputs by roots must extend to at least 11 m depth. Fine root biomass declined to only 0.1 g/cm^3 at 3 m depth and was relatively constant from 3 to 6 m depth (Fig. 5), but we do not know whether it remains constant below 6 m or at what depth it declines further. In any case, fine root biomass apparently was sufficient to extract significant amounts of water to about 18 m and to impart an isotopic signature on soil $^{13}CO_2$ and $^{14}CO_2$ throughout the measured 11 m profiles.

Previous research has demonstrated that the source of deep soil CO_2 is predominantly root respiration and decomposition of roots (Trumbore et al. 1995, 2006). The flux of dissolved organic carbon below 25 cm depth was shown to be trivial (1–2 g C m^{-2} year^{-1}) in similar deep Oxisols of the region (Markewitz et al. 2004). Fine root production has been estimated for deep soils (1–6 m) of the eastern Amazon forest on the order of only 20–30 g C m^{-2} year^{-1} (Trumbore et al. 2006), which is about 3 orders of magnitude smaller than soil organic matter stocks. Most of the soil organic matter is highly depleted in radiocarbon, indicating that it has remained isolated from actively cycling C pools for centuries or millennia (Trumbore et al. 1995). Only a small fraction of deep soil C, predominantly derived from roots, is actively exchanging with atmospheric CO_2 on time scales of decades or less. Because of low rates of diffusion in deep soils, CO_2 concentrations increase with depth, but the rates of CO_2 production decrease with depth in proportion to root biomass (Davidson et al. 2004). Production of CO_2 below 1 m depth was on the order of 80–200 g C m^{-2} year^{-1}, which was 8–20% of the efflux from the soil surface (Davidson et al. 2004). In summary, deep roots contribute a small amount of annual inputs of C to deep soil and also make a modest, but important, contribution to total soil CO_2 production.

Although inputs of organic C to deep soils may be small with respect to the carbon dynamics of the forest, the deep rooting habit has other important ecosystem implications. For example, the deep soil CO_2 production may be an important biogenic source of acidity, which affects weathering rates over long time scales (Richter and Markewitz 1995). Here we have shown that deep roots also clearly affect the ecosystem water balance, which is crucial for the survival strategy of the vegetation in a seasonally dry forests (Nepstad et al. 1994). Although deep roots were not abundant, they accessed important quantities of soil water to about 18 m depth in this study.

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