Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake

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Summary

• Deep root water uptake in tropical Amazonian forests has been a major discovery during the last 15 yr. However, the effects of extended droughts, which may increase with climate change, on deep soil moisture utilization remain uncertain.

• The current study utilized a 1999–2005 record of volumetric water content (VWC) under a throughfall exclusion experiment to calibrate a one-dimensional model of the hydrologic system to estimate VWC, and to quantify the rate of root uptake through 11.5 m of soil.

• Simulations with root uptake compensation had a relative root mean square error (RRMSE) of 11% at 0–40 cm and < 5% at 350–1150 cm. The simulated contribution of deep root uptake under the control was *c.* 20% of water demand from 250 to 550 cm and *c.* 10% from 550 to 1150 cm. Furthermore, in years 2 (2001) and 3 (2002) of throughfall exclusion, deep root uptake increased as soil moisture was available but then declined to near zero in deep layers in 2003 and 2004.

• Deep root uptake was limited despite high VWC (i.e. > 0.30 cm^3 cm^{-3}). This limitation may partly be attributable to high residual water contents (θ_r) in these high-clay (70–90%) soils or due to high soil-to-root resistance. The ability of deep roots and soils to contribute increasing amounts of water with extended drought will be limited.

Introduction

The role of deep root uptake of water in the lowland tropical forests of the Amazon has been a major discovery during the last 15 yr (Nepstad *et al.*, 1994; Hodnett *et al.*, 1996). Evidence of soil moisture depletion to depths of 18 m, inferred to be a function of root uptake, has recently been reported in an Amazonian forest (Davidson *et al.*, 2009). This deep root uptake of moisture is responsible for the maintenance of an evergreen canopy in Amazonian lowland tropical forests despite a 5- to 6-month dry season in parts of the Amazon basin or during short-term droughts (Saleska *et al.*, 2007; though see also Anderson *et al.*, 2010). The effects of extended drought, which may increase with changing climate (Timmermann *et al.*, 1999; Werth & Avissar, 2001), on deep soil moisture utilization remain uncertain, although they have recently been investigated through experimentally simulated drought (Nepstad *et al.*, 2002, 2007; Fisher *et al.*, 2006, 2007; Brando *et al.*, 2008).

To study the response of humid Amazonian forest to severe drought, two partial throughfall exclusion experiments were recently conducted, one from 2001 to the present in the Caxiuanã National Forest, Pará, Brazil (da Costa *et al.*, 2010) and the other from 1999 to 2005 in the Tapajós National Forest, Santarém, Brazil (Nepstad *et al.*, 2002). Approximately 60 ± 10% of incoming throughfall was diverted from the soil surface in the 'exclusion' plots. Previously reported results from the Tapajós demonstrated impacts in the exclusion plot that included increased tree mortality (Nepstad *et al.*, 2007), altered trace gas fluxes (Davidson *et al.*, 2008), and decreased net primary productivity (NPP) (Brando *et al.*, 2008). A similar decrease in gross primary productivity (GPP) was observed in Caxiuanã along with a decrease in soil CO_2 efflux (Fisher *et al.*, 2007;

Sotta *et al.*, 2007). All these changes in both locations were coincident with soil water depletion in the exclusion plots measured through 5 or 11 m depth for Caxiuanã and Tapajós, respectively (Fisher *et al.*, 2007; Brando *et al.*, 2008).

Although these observed soil moisture depletions under throughfall exclusion clearly demonstrate a change in soil moisture storage, the rate of root uptake from each soil layer cannot be directly estimated because water fluxes into each layer from above or out of each layer from below are not quantified. To account for these fluxes, modeling analyses have been undertaken to fully quantify the hydrologic system (Belk *et al.*, 2007; Fisher *et al.*, 2007). These previous efforts with one-dimensional models have sufficiently described the observed volumetric water content data and have indicated a critical role for deep soils and deep root uptake through 3 and 11 m in Caxiuanã and Tapajós, respectively. At Caxiuanã, low soil water potentials and a high soil-to-root water resistance were inferred to be the critical controllers of plant water uptake (Fisher *et al.*, 2007). At Tapajós, deep root uptake was demonstrated to be critical in sustaining evapotranspiration during the first 2 yr of exclusion (Belk *et al.*, 2007).

Most recently, however, two processes of soil water movement have been demonstrated at Tapajós that call into question the exact mechanism of deep root uptake in these moist tropical forests. The first is the demonstration of hydraulic root redistribution in these lowland tropical forests (Rocha *et al.*, 2004; Oliveira *et al.*, 2005). Hydraulic root redistribution in the upward direction (i.e. hydraulic lift) results from the movement of water by roots from deeper moister soil horizons to drier surface soil horizons, with subsequent uptake of this water to meet transpirational demand. Small increases (c. 0.01 cm^3 cm^{-3}) in soil moisture in the upper 40 cm of a nearby forest at Tapajós were measured after nighttime hydraulic lift (Rocha *et al.*, 2004). Within the Tapajós throughfall exclusion experiment, not only was hydraulic root redistribution evident in the upward direction but sap flux sensors indicated periods of water flow down roots from shallow to deeper soil layers (Oliveira *et al.*, 2005). These demonstrations of hydraulic redistribution in moist environments are novel and were rapidly incorporated into global circulation models (GCMs), which historically have used a < 2 m soil profile and thus assume water limitation to plant growth through much of the year (Lee *et al.*, 2005). Although the process of hydraulic lift appears to be well established in these moist lowland tropical forests, the quantity of water that can be redistributed through this process is not well quantified. In the GCM simulation of Lee *et al.* (2005) redistribution was suggested to increase evapotranspiration by as much as 40%, although there was no means to validate this estimation.

A second potential mechanism of water redistribution was suggested by a deuterium tracer study within the

Tapajós exclusion experiment (Romero-Saltos *et al.*, 2005). In this study the deuterium signal, which typically moves down through the soil profile, was shown to rise 64 cm in the soil of the control plot during the dry season. Although a rise of the deuterium tracer was not measured in the exclusion plot because of limited initial downward movement of the deuterium label, similar processes were presumed to exist. A rise in deuterium could result if surface soils were sufficiently depleted of water from root water uptake that the hydraulic gradient was in the upward direction (Marshall *et al.* 1996). It is therefore possible that during the dry season water uptake was maintained in the surface not through hydraulic lift but through capillary rise.

Given the recent evidence for these soil water movement mechanisms in humid environments and the availability of four new years of volumetric water content (VWC) data at the Tapajós location that include three additional years of throughfall exclusion, the objective of this study was to test the ability of a one-dimensional hydrologic model to accurately predict this 7-yr record of VWC data through 11.5 m of soil beneath both the control and throughfall exclusion plots. Furthermore, this complete hydrologic accounting will allow for quantitative estimation of deep soil root water uptake within discrete layers during the Tapajós experiment.

Materials and Methods

Site description

The experiment being modeled was carried out in the Tapajós National Forest, Pará, Brazil (2.8979°S, 54.9528°W). The site is located c. 150 m above and 13 km east of the Tapajós River and has c. 200 cm of rainfall annually (Nepstad *et al.*, 2002). The Tapajós throughfall exclusion experiment consisted of two structurally and floristically similar 1-ha plots: an 'exclusion plot' and a 'control plot'. The plots are situated on a relatively level, upper-landscape plateau position where the soils are predominantly Haplustox (Latossolos vermelhos) dominated by kaolinite clays, and support a *terra firma* forest, which is a dense, humid, evergreen forest that does not flood annually. The throughfall reduction experiment was initiated in 1998. After a 1-yr pretreatment period without exclusion, a 'roof' of plastic panels 1–2 m above the soil surface was utilized to divert c. 30–40% of annual incoming precipitation after it had passed through the canopy (i.e. throughfall) during the rainy seasons (i.e. January–June) for 2000–2004. Panels were removed during the dry season and re-installed the following year. In 2005, measurements continued but panels were not installed for a 1-yr recovery period. More complete details of the experimental design have been published elsewhere (Nepstad *et al.*, 2002; Brando *et al.*, 2008).

Site-specific data

Many water balance components were collected throughout this multi-year, multi-investigator experiment. Furthermore, many components of the hydrologic model were described previously by Belk *et al.* (2007). Citations are therefore provided with minimal additional descriptions for data sources that have been previously published, while components that are specific to the current modeling effort are described in greater detail.

Rainfall inputs were measured nearly daily at two to four locations throughout the experiment and daily (Nepstad *et al.*, 2002; Brando *et al.*, 2008), monthly (Oliveira *et al.*, 2005; Davidson *et al.*, 2008), and annual (Nepstad *et al.*, 2007) representations are available. The quantitative fraction of throughfall exclusion was also estimated periodically throughout the study and ranged from 60 to 70% (Nepstad *et al.*, 2002; Davidson *et al.*, 2009).

VWCs (cm^3 cm^{-3}) were measured using time domain reflectometry (TDR) (Topp *et al.* 1980) sensors installed vertically from 0 to 30 cm and horizontally at 0.5 and 1 m and then at 1-m intervals to 11-m depth in five soil shafts (two plots; five shafts per plot; yielding 10 sensors per depth for both plots). Each soil shaft extends to a depth of 12 m and access was obtained using a system of wooden beams and supports. Details of TDR construction and calibration have previously been provided (Jipp *et al.*, 1998; Nepstad *et al.*, 2002; Belk *et al.*, 2007). Waveforms from the TDR sensors were collected approximately once per month. Various years, depths, and integrated depth averages of VWC and plant available water (PAW) estimates based on VWC have previously been reported (Nepstad *et al.*, 2002; Davidson *et al.*, 2004, 2008, 2009; Oliveira *et al.*, 2005; Belk *et al.*, 2007; Brando *et al.*, 2008).

Saturated hydraulic conductivity (K_s) was quantified at 0.15, 0.30, 0.5, 1, 2, 3, and 4 m using a Guelph permeameter (SoilMoisture Equipment Corp., Santa Barbara, CA, USA). Details are provided in Belk *et al.* (2007). K_s results at the surface and at 30 cm were arithmetically averaged and used to approximate saturated flow rates in the first model layer. The other field measurements were assigned to the closest layer midpoint. For depths > 4 m, a power function was fit through the data and point estimates of K_s were extrapolated to 11 m. Unsaturated hydraulic conductivity ($K(\theta)$) was calculated from K_s values according to the nonlinear equation of Mualem (1976) and a pore connectivity of 0.5 was assumed:

$$K(\theta) = K_s \Theta^{1/2} [1 - [1 - \Theta^{n/(n-1)}]^m]^2 \qquad \text{Eqn 1}$$

Soil water retention data were generated for field samples within all VWC layers (Belk *et al.*, 2007). A standard pressure plate method was used with n = 4 soil cores per depth and pressures of 0.01–1.5 MPa (Klute & Dirksen, 1986).

The van Genuchten parameters (θ_s, θ_r, α, and n) for the soil moisture characteristic (SMC) functions were fit to these data using nonlinear regression (Wraith *et al.*, 1993). In view of previous modeling difficulties with the fits to these measured values (Belk *et al.*, 2007) an inverse solution for θ_s, θ_r, α, and n was also utilized. Soil values were optimized within HYDRUS® (Prague, Czech Republic) using an inverse model solution to provide a best fit for the available VWC data (Šimůnek *et al.*, 2006). Each layer was fit individually, with all layers being optimized a second or third time after the optimization of all layers to check for any changes.

Fine-root (0–2 mm diameter) biomass data were determined at 0–0.1, 0.5, 1, 2, 3, 4, 5, and 6 m (Belk *et al.*, 2007; Davidson *et al.*, 2009). The fraction of the total fine (live) root biomass (0–2 mm) in each layer was used to partition root water uptake (i.e. a rooting factor, $R(z)$) for each modeled soil layer. The root biomass was considered to be 10% less than the horizon above for estimating root factors below 6 m (Belk *et al.*, 2007).

Potential evapotranspiration (PET) was previously calculated for the exclusion experiment using the Thornthwaite method (Thornthwaite & Mather 1957) and onsite monthly temperature inputs (Belk *et al.*, 2007). Recently, direct measures of actual evapotranspiration (AET) have become available from an eddy-flux tower situated within 1.5 km of the exclusion experiment (Hutyra *et al.*, 2007). Monthly, 24-h averages of AET measured for 2002–2005 were utilized for these years. To estimate AET from 1999 to 2002, an average daytime temperature–AET regression (r^2 = 0.63) was developed using the eddy-flux tower data. Thereafter, available onsite daytime forest canopy temperature data (Belk *et al.*, 2007) were used to create a time series for AET (Fig. 1). In the model, PET is set equal to the measured AET. In the absence of soil water limitations, the resulting simulated AET should therefore closely approximate the measured AET.

Soil water model

The onsite data collected as described in the previous section largely served as input variables for numerical modeling of water flow through the soil profile, with the VWC data serving as the calibration data (Fig. 2). Vertical water movement through soil layers is driven by the difference in total soil hydraulic head, which integrates the effect of matric and gravitational forces. The Richards equation for saturated and unsaturated water flow was utilized to determine fluxes and a sink term was incorporated to account for water uptake by plant roots (Šimůnek *et al.*, 2006). Although a similar mathematical structure was used previously (Belk *et al.*, 2007), currently version 1.1 of HYDRUS® (2D/3D) was utilized for solving the flow equations. Simulations were performed for the control plot with no reduction in throughfall inputs and for the exclusion plot using

Fig. 1 Monthly precipitation (bars) and mean monthly actual evapotranspiration (AET; points) at the throughfall exclusion experiment in the Tapajos National Forest, Santarem, Brazil. Precipitation was measured on site while mean daily AET for each month was measured for 2002–2005 in a nearby eddy-flux tower but estimated for 1999–2001 based on temperature using a temperature–AET regression from the nearby eddy-flux measurements.
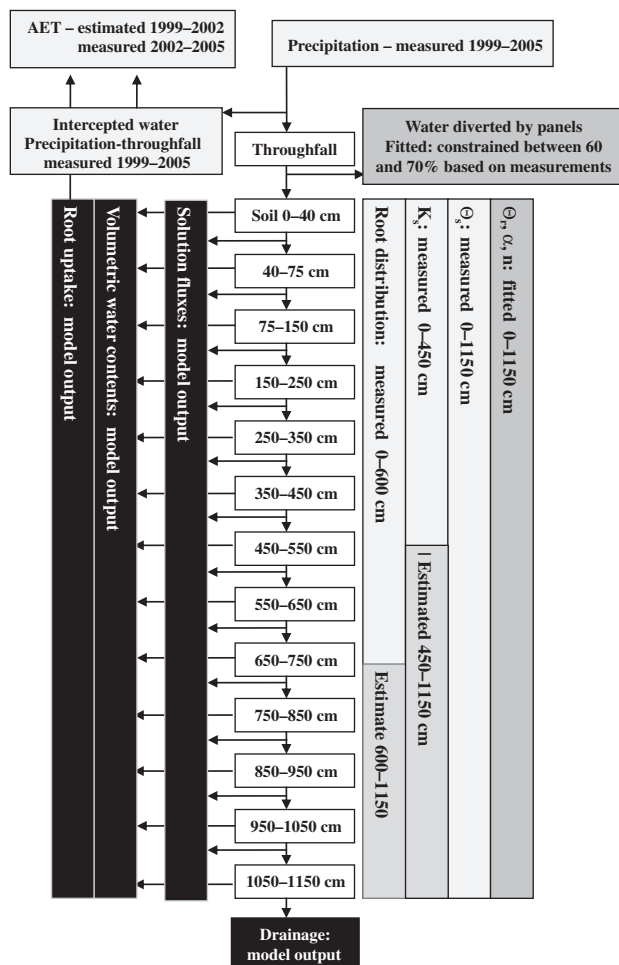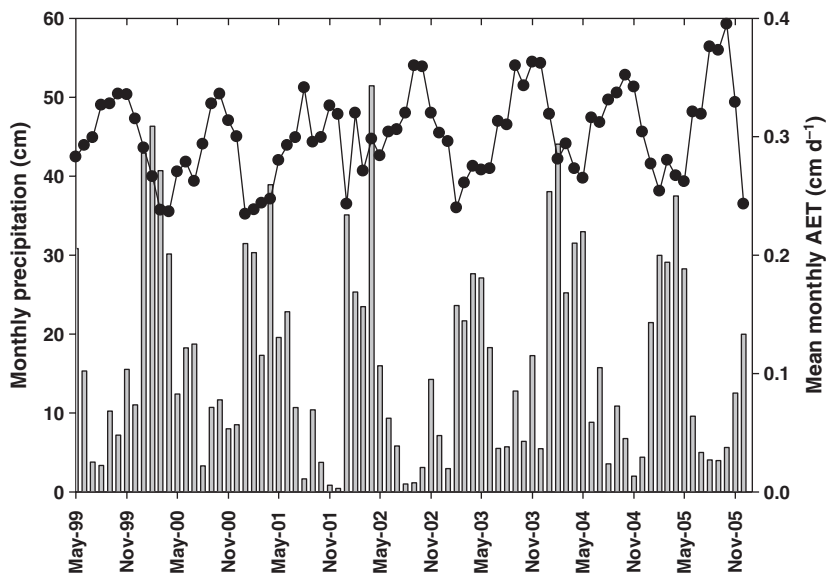

Fig. 2 Model structure used in HYDRUS®. Shading from light to dark includes measured, estimated, fitted, and output values, respectively. AET, actual evapotranspiration.

throughfall exclusion during the rainy season. The percentage of throughfall exclusion was constrained to be between 60 and 70% based on the field observations with a single percentage being fit based on a minimization of the root mean square error between observed and predicted VWCs in each layer and the fit to the total water content in the 11.5-m profile.

The model was structured to simulate 13 soil layers (i.e. 0–0.4, 0.4–0.75, 0.75–1.5, 1.5–2.5, 2.5–3.5, 3.5–4.5, 4.5–5.5, 5.5–6.5, 6.5–7.5, 7.5–8.5, 8.5–9.5, 9.5–10.5, and 10.5–11.5 m) which were chosen so that the TDR probes would be near the midpoints of each layer. Vertical discretization (Δz) was 1 cm for 0–5 cm; 2 cm for 5–40 cm; 2.5 cm for 40–75 cm; 5 cm for 75–150 cm; and 10 cm thereafter to 1150 cm. Temporal discretization (Δt) ranges from 10^{-5} of a day to 1 d and depends on the size of the pressure gradient between layers, with larger gradients requiring smaller time steps.

Water input to the upper boundary layer of soil was based on the precipitation inputs minus canopy interception, which was empirically determined to be 12 ± 2% (Belk *et al.*, 2007). This empirical relationship did not vary by season and data were not available to test a relationship with rainfall intensity. When the treatment plot was simulated, the throughfall input was diverted from the soil when the panels were in place. Water reaching the soil surface infiltrated directly into the uppermost soil layer because the measured surface infiltration rates were high (> 30×10^{-6} m s^{-1}).

All 13 layers hold a depth of water (D_w, cm) equivalent to the soil moisture within that increment of soil. The water depth in each layer was initialized using measured soil water content data from 17 May 1999, the first day of simulation.

The water content of each layer in $cm^3\ cm^{-3}$ was determined using the depth of water (D_w, cm) and the soil thickness (Δz; cm):

$$\theta(z) = \frac{D_w(z)}{\Delta z} \qquad \text{Eqn 2}$$

Water flux between soil layers was determined using Darcy's law for one-dimensional (vertical), unsaturated flow (Muller 1999) where the total hydraulic head of the soil water ($H(z)$) in a given layer is the sum of the matric (h_m) and gravitational (h_z) heads. The matric head of the soil water was determined using the van Genuchten equation relating water content to matric head (van Genuchten 1980):

$$h_m = \frac{1}{\alpha}\left[\left[\frac{(\theta - \theta_r)}{\theta_s - \theta_r}\right]^{-1/m} - 1\right]^{1/n} \qquad \text{Eqn 3}$$

where θ_s is the saturated water content, θ_r is the residual water content and the fraction describes the relative saturation of the soil ($cm^3\ cm^{-3}$), and α (m^{-1}), n, and $m = 1 - 1/n$ are fitting parameters.

Changes in soil water storage were modeled using the Richards (mass balance) equation that accounts for inflows and outflows in each layer:

$$\frac{\partial q_z(z)}{\partial z} \mp U(z) = \frac{\partial \theta(z)}{\partial(t)} \qquad \text{Eqn 4}$$

($U(z)$, internal sources or sinks within each layer.) Root uptake (Eqn 5) is the only mechanism for internal water loss within each layer in the current model.

The model assumes that there is no evaporation from the soil surface and that water required for transpiration by vegetation is removed from each soil layer before downward percolation is allowed. Water is removed from the soil in an amount equal to PET after evaporation of intercepted precipitation. If the volume of interception exceeded PET, demand for soil water was zero for that day. On days without precipitation PET is met only through soil water uptake. The fraction of this total uptake extracted from a given layer is:

$$U(z) = U_{max}R(z)\text{URF}(z) \qquad \text{Eqn 5}$$

(U_{max}, the maximum amount of water extracted from the soil; $R(z)$, the proportion of fine-root biomass in layer z; URF(z), an uptake reduction factor that restricts plant uptake in layer z based on the matric head.) The URF is based on matric head following the formulation of Feddes *et al.* (1978, 2001), in which water uptake is considered optimal between pressure heads h2 (0.01 MPa) and h3

(0.3 MPa) and then decreases (or increases) linearly with pressure head between h3 and h4 (1.5 MPa). When the matric head exceeds h3 such that root water uptake is reduced in drying parts of the root zone, uptake can be compensated by increased uptake from other parts of the root zone (Šimůnek & Hopmans, 2009). The extent of compensation is set between 0 and 1, with 0 being full compensation. Even under full compensation as used here, evapotranspiration will decline as all layers drydown below h3. We evaluated the role of deep root uptake in the model both with and without uptake compensation. Root uptake from each soil layer was estimated as the difference between flux into a layer and the flux out, and change in soil storage.

Results

Model calibration

Model fits were constrained to interception values between 10 and 14% and exclusion between 60 and 70% based on on-site empirical data. Use of measured evapotranspiration from the nearby eddy-flux tower was also a constraint to the model. Finally, the exclusion treatment provided additional constraints in requiring some reduction in evapotranspiration during 2002–2004. Within these limits, models were calibrated to VWC ($cm^3\ cm^{-3}$) and total water content in the soil profile (cm) through all 13 layers. In the control plot, using the model with full root uptake compensation, the range of interception values had only a minor influence on calibration fits or the distribution of root uptake. Increasing interception served to increase the amount of evapotranspiration that was satisfied by canopy evaporation, decrease the amount of evapotranspiration satisfied by root uptake, and decrease drainage (Table 1). Given the limited change in the control plot calibrations, the mean 12% interception was utilized. In the treatment plot, the model with full root uptake compensation and 12% interception was calibrated with 60–70% throughfall exclusion. Exclusion of

Table 1 Hydrologic outputs for model simulations with varying percentage of rainfall interception under the control plot of the throughfall exclusion experiment in the Tapajós National Forest, Brazil

Component	% interception		
	10	12	14
Interception ET	91	99	107
Root uptake	580	570	562
AET	670	670	670
Drainage	613	597	579

Fluxes are for the entire simulation for May 1999 to December 2005.
Interception ET, evapotranspiration resulting from evaporation of rainfall intercepted in the canopy; AET, actual evapotranspiration; Drainage, water draining from the bottom of the 11.5-m soil profile.

68% provided slightly better fits to the VWC data and the best regression fit to the profile water content data (r^2 = 0.77 for 68% vs 0.69 and 0.76 for 60 and 70% exclusion, respectively).

Soil moisture characteristic curves

Within these calibrated models (12% interception and 68% exclusion with full root uptake compensation) the inverse solution for the parameters (θ_s, θ_r, α, and n) of the soil moisture characteristic curves demonstrated similar patterns for control and treatment plots (Table 2). Without uptake compensation the patterns were the same and absolute values of θ_s, θ_r, α, and n varied by < 4% in all cases. The predicted parameters are within the range of values estimated for a broad tropical soil data set (Hodnett & Tomasella, 2002). Measured soil saturation water content (θ_s) had a relatively small range (0.31–0.45 cm^3 cm^{-3}) across all soil depths, while optimized residual soil water content values (θ_r) had a greater range (0.18–0.37 cm^3 cm^{-3}), with the lowest values being in the upper 200 cm. These inverse solutions for θ_r differed from the previously calibrated parameters reported in Belk *et al.* (2007) with the greatest differences (i.e. 0.3 vs 0.2 cm^3 cm^{-3}) being at depth (600–1100 cm). The currently simulated results retain greater water content (i.e. θ_s > 0.30 cm^3 cm^{-3}), which is consistent with laboratory-generated pressure plate data (see Fig. 5 in Belk *et al.*, 2007) and the measured VWCs, which never decreased below 0.30 cm^3 cm^{-3} in the 450–1150-cm layers.

Alternative models

In general, the one-dimensional model simulations with or without uptake compensation or even without roots below 5 m succeeded in capturing many of the details of the VWC measurements under the control conditions (Fig. 3a,b). Over the full record of simulation the root mean square error [RMSE $= \sqrt{\frac{\Sigma((\text{PredictedVWC}-\text{ObservedVWC})^2)}{n}}$] in soil moisture for the control ranged from 0.015 to 0.038 cm^3 cm^{-3} depending on soil layer. On a relative basis (i.e. relative root mean square error [RRMSE $=(\frac{\text{RMSE}}{(\Sigma VWC/n)}) \times 100$]) this error was greatest in the surface 0–40-cm layer (11.3%) (Table 3) but was < 8.4% in all other cases and improved with depth where variance in VWC was lower (Table 3). These same data have coefficients of determination for a linear regression between observed and predicted VWCs of > 0.48 in the upper 350 cm (e.g. r^2 = 0.56, 0.48, 0.61, 0.56, and 0.60 for 40, 75, 150, 250, and 350-cm layers in the control plot). Below 350 cm, coefficients of determination ranged from 0.36 to 0.10. Although simulated VWC was relatively good within all models, the modeled evapotranspiration was most similar to the observed evapotranspiration in the calibration model with root uptake compensation, suggesting some limitation to extraction of sufficient water in the other models (Table 3). This limitation in evapotranspiration was even more evident in the treatment calibrations where observed soil moisture depletion at depth was not well predicted in the absence of uptake compensation or roots below 5 m (Fig. 3c,d). Root mean square error (RMSE) ranged up to 0.045 cm^3 cm^{-3} at 950 cm in the absence of deep roots and relative root mean square error (RRMSE) was greater without root uptake compensation or without roots below 5 m in all layers below 750 cm (Table 3). For the calibration model, in the exclusion plot, r^2 for predicted vs observed was 0.56, 0.64, 0.55, 0.61, 0.58, 0.72, 0.75, and 0.76 for the eight layers from 450 to 1150 cm.

Using the calibration with root uptake compensation, the observed VWCs were well modeled throughout the entire

Table 2 Inverse solution (± 1 SE) for van Genuchten parameters of soil saturation water content (θ_s), residual soil water content (θ_r), and fitting parameters α and n to represent soil moisture characteristic curve under control and treatment conditions

| Layer (cm)	θ_s (cm^3 cm^{-3})		θ_r (cm^3 cm^{-3})		α (cm^{-1})		n	
	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
0–40	0.442 ± 0.033	0.402 ± 0.031	0.214 ± 0.013	0.180 ± 0.011	0.006 ± 0.001	0.006 ± 0.002	1.94 ± 0.13	1.99 ± 0.27
75	0.344 ± 0.014	0.311 ± 0.018	0.222 ± 0.008	0.208 ± 0.004	0.008 ± 0.001	0.008 ± 0.003	1.82 ± 0.13	1.99 ± 0.18
100	0.355 ± 0.007	0.349 ± 0.013	0.247 ± 0.005	0.232 ± 0.006	0.009 ± 0.002	0.010 ± .002	1.97 ± 0.22	1.99 ± 0.21
200	0.342 ± 0.007	0.316 ± 0.005	0.225 ± 0.007	0.224 ± 0.006	0.014 ± 0.002	0.008 ± 0.001	1.51 ± 0.10	1.51 ± 0.11
300	0.370 ± 0.011	0.336 ± 0.005	0.260 ± 0.005	0.231 ± 0.010	0.009 ± 0.004	0.013 ± 0.005	1.70 ± 0.17	1.22 ± 0.02
400	0.387 ± 0.011	0.409 ± 0.019	0.273 ± 0.017	0.287 ± 0.014	0.007 ± 0.007	0.008 ± 0.004	1.78 ± 0.64	1.85 ± 0.36
500	0.421 ± 0.009	0.402 ± 0.012	0.324 ± 0.026	0.309 ± 0.007	0.008 ± 0.005	0.012 ± 0.008	1.56 ± 0.48	1.49 ± 0.11
600	0.426 ± 0.010	0.426 ± 0.016	0.356 ± 0.014	0.344 ± 0.008	0.009 ± 0.009	0.015 ± 0.008	1.58 ± 0.38	1.40 ± 0.11
700	0.435 ± 0.009	0.420 ± 0.014	0.365 ± 0.041	0.341 ± 0.011	0.009 ± 0.010	0.010 ± 0.006	1.66 ± 0.61	1.30 ± 0.05
800	0.435 ± 0.010	0.425 ± 0.049	0.365 ± 0.016	0.331 ± 0.037	0.009 ± 0.014	0.002 ± 0.004	1.51 ± 0.35	1.28 ± 0.16
900	0.427 ± 0.020	0.425 ± 0.033	0.368 ± 0.039	0.280 ± 0.064	0.001 ± 0.002	0.0002 ± 0.0000	1.44 ± 0.64	1.37 ± 0.26
1000	0.428 ± 0.022	0.435 ± 0.012	0.362 ± 0.057	0.302 ± 0.009	0.001 ± 0.001	0.006 ± 0.002	1.43 ± 0.91	1.28 ± 0.49
1100	0.425 ± 0.021	0.422 ± 0.004	0.361 ± 0.023	0.323 ± 0.007	0.0003 ± 0.0002	0.004 ± 0.003	1.98 ± 0.71	1.55 ± 0.07
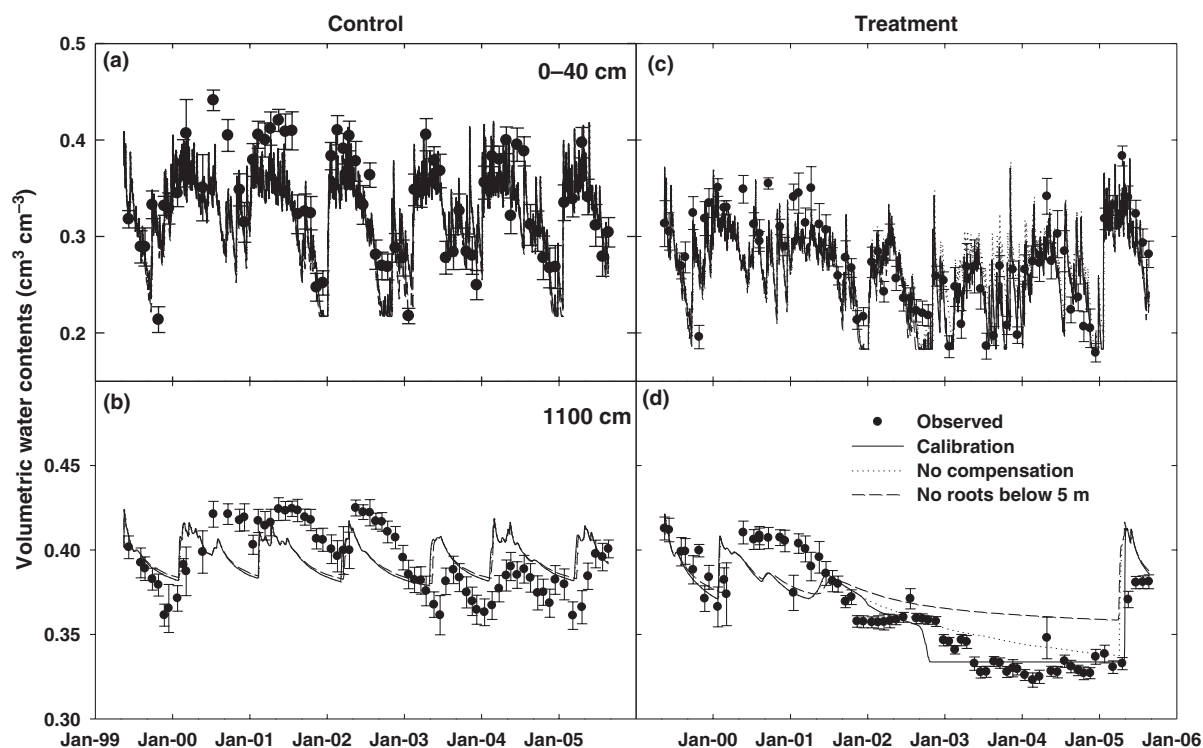
Fig. 3 Measured (circles; mean ± 1 SD) and simulated (line) volumetric water contents for control (a, b) and exclusion (c, d) plots at the top (0–40 cm) and bottom (1100 cm) of the soil profile under three alternative simulation models for the throughfall exclusion experiment in the Tapajo's National Forest, Brazil.

Table 3 Relative root mean square error (%) for the calibration model, calibration model without root uptake compensation, and calibration model without roots below 5 m under control and treatment conditions

	Control			Treatment		
	Calibration	No compensation	No root below 5 m	Calibration	No compensation	No root below 5 m
0–30	11.3	11.4	11.4	11.5	13.0	12.1
75	8.4	8.4	8.5	6.4	6.6	6.7
150	6.4	6.4	6.7	7.8	8.6	8.3
250	6.6	6.6	6.6	5.2	6.4	5.2
350	5.8	5.8	5.8	6.2	6.9	6.1
450	7.5	7.8	7.5	6.9	7.8	7.6
550	5.4	5.5	5.4	4.7	4.7	4.5
650	4.7	4.7	4.5	4.3	4.8	4.2
750	4.7	4.7	4.4	3.5	3.8	4.3
850	4.6	4.7	4.4	5.5	6.7	9.0
950	3.7	3.7	3.7	6.2	9.1	11.8
1050	4.9	4.8	4.7	5.0	6.8	9.5
1150	5.2	5.2	5.1	3.7	4.7	6.5
AET (cm)[1]	670	645	660	640	624	616
% MAET	98	94	96	93	91	90

[1]The last two rows show modeled actual evapotranspiration (AET) estimated by each alternative model and model AET as a percentage of measured tower actual evapotranspiration (%MAET) for control and treatment conditions under the throughfall exclusion experiment in the Tapajo's National Forest, Brazil (1999–2005).

profile in both the control and treatment conditions (Figs 4, 5). In the upper portions of the profile (0–200 cm) the simulations captured the temporal dynamics and were rarely biased high or low, although under both control and treatment plots the RRMSE was slightly greater than in the lower portions of the profile (Table 3). In the lower

portions of the profile, despite the lower RRMSE, simulations were periodically biased high or low for multiple months (e.g. 700 cm under control in Fig. 4b), although the absolute difference was quite small. Some of these biases resulted from a decline in the maximum VWC contents observed over the record, particularly in the control plot. After a natural drought through late 2002 and most of 2003, VWC in all profile layers below 100 cm never achieved maximal values observed previously, despite above average rainfall in 2004 and early 2005. If there was a fundamental shift in soil physical structure, for example, increased porosity as a result of soil cracking or an increase in entrapped air as a result of extreme soil drying, this type of step function would not be well captured by the present model. Unfortunately, it is unclear if these data reflect naturally occurring processes or are a measurement artifact resulting, for example, from loss of soil contact around TDR probes. Regardless, the inverse solution fits the mean response of the entire data set and thus underestimates the early observations and overestimates the later observations (Fig. 4b). Again, however, the absolute errors are small and the temporal dynamics are reasonable.

Root uptake

Utilizing the model calibration with uptake compensation, during the first 3 yr (1999–2001) of the exclusion experiment modeled root uptake from the entire profile was similar under control and exclusion plots (Fig. 6, Table 4). Only in 2002 did the cumulative modeled uptake begin to diverge such that modeled AET < measured AET in the exclusion plot. Under control conditions, c. 36 ± 3% of total modeled uptake was from the 0–40-cm layer while c. 91 ± 1% of uptake was contributed by the 0–550-cm layer, with the final 9% coming from the 550–1150-cm layer. Under exclusion, the percentage contribution to modeled root uptake during 2002–2004 increased in the upper layers to 48 ± 12% and 94 ± 11% in the 0–40 and 0–550-cm layers, respectively. Although there was an increase in the relative modeled root water uptake from the deepest layers (750–1150 cm) in 2001 and 2002 under exclusion, this increase appeared to deplete the available soil water, as uptake from these layers declined to near zero the following 2 yr (Table 4). Contrary to expectations of an increased reliance on deep root uptake with increased soil drying during the exclusion, the model simulated a greater percentage contribution from the upper soil layers.

Over the entire study, VWC was predicted within 11% or less in each layer and the profile water content was predicted within 4.5 and 3.2% RRMSE for control and exclusion, respectively (Fig. 7). Coefficients of determination for a linear regression (i.e. r^2) of observed vs predicted whole profile water contents presented in Fig. 7 were 0.37 and 0.72 for control and treatment, respectively.

Annual water balance

During the complete water years of 2000–2004, modeled AET in the control plot averaged 99.7 ± 0.3% of AET measured at the nearby eddy-flux tower, which ranged from 104 to 114 cm yr^{-1} (Table 5). In the exclusion plot, modeled AET averaged 94.6 ± 5.0% of the measured tower AET with a declining trend over time. In 2000, modeled AET in the exclusion plot was 99.3% of the measured tower AET while in 2003 the exclusion plot achieved only 86.9% of measured tower AET. After the natural 2003 drought, AET in the exclusion plot recovered slightly in 2004 to 92.8% of the measured tower AET. Runoff (i.e. drainage out of the bottom of the profile) also differed between the two plots. In the control plot, drainage ranged from 135 to 41 cm yr^{-1}, accounting for 55 to 24% of precipitation (or 61 to 27% of throughfall). The lowest runoff year was observed in the 2003 drought. In the exclusion plot, drainage was 36% of throughfall (i.e. 48 cm) during the first year of exclusion but declined to 0% or 0 cm in both 2003 and 2004.

Discussion

Mechanisms of water flux

As was observed after the first 3 yr of the Tapajós exclusion experiment (Belk et al., 2007), a one-dimensional hydrologic model using unsaturated flow accurately simulated VWC over the entire soil profile. In the Caxiuanã exclusion study, a similar physically based one-dimensional model also successfully simulated observed VWC (Fisher et al., 2007). In Caxiuanã, coefficients of determination between observed and predicted VWCs for the upper 3 m of the profile over 3 yr were 0.87 and 0.68 for control and treatment, respectively. At Tapajós, over the entire study, whole profile water contents were well predicted (Fig. 7), although the strong drought in 2003 clearly affected the goodness of fit of the model under the control. Nonetheless, under control conditions at Tapajós the model accurately simulated measured AET (Table 3) and the relative proportion of drainage to precipitation was well within the range of 18–63% previously reported for watershed studies in the Amazon (Bruijnzeel, 1990; Markewitz et al., 2006)

During these simulations, capillary rise (i.e. an upward hydraulic flux) was never induced across any of the lower layer boundaries even under the exclusion. Capillary rise was suggested by a deuterium tracer study within the Tapajós exclusion experiment and was estimated to account for as much as 32 cm of water moving up through the upper 240 cm of soil (Romero-Saltos et al., 2005). Capillary rise is possible within the HYDRUS® model architecture and can be induced, for example, if root uptake is restricted to the upper two soil layers, but then model fits with VWC through the profile are quite poor (data not
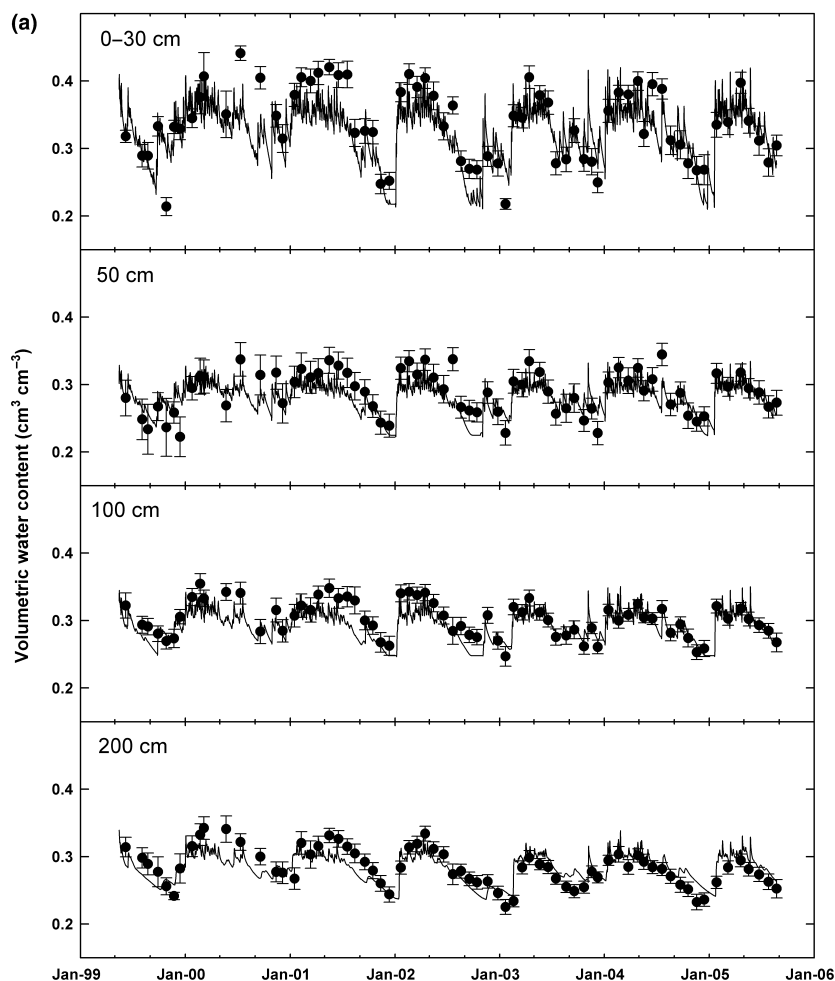
(a)

Fig. 4 Measured (circles; mean ± 1 SD) and simulated (line) volumetric water contents for (a) 0–200 cm and (b) 300–1100 cm under the control plot of the throughfall exclusion experiment in the Tapajo's National Forest, Brazil.

shown). At Caxiuanã, capillary rise as a source of water to balance the water budget in the 5-m instrumented portion of the profile was not discussed (Fisher *et al.*, 2006, 2007, 2008). Given the current model results it does not appear that large volumes of water are migrating upward through the profile as a result of capillary rise, although some mechanism for deuterium movement is occurring (e.g. gaseous phase movement or diffusion in biofilms).

The current simulation model did not include a mechanism for moving water through root redistribution. Although there is strong evidence for hydraulic redistribution in this location (Rocha *et al.*, 2004; Oliveira *et al.*, 2005) and others (Caldwell *et al.*, 1998; Domec *et al.*, 2010), the amount of water moved by these processes has rarely been quantified (Jackson *et al.*, 2000; Ryel *et al.*, 2002). The current results suggest that large volumes of hydraulic redistribution are not needed to accurately simulate VWC in either upper or lower layers. In the 0–40-cm layer, where relative errors in θ were greatest (i.e. 11%), the absolute water depth difference was < 1.5 cm and in the lower layers relative differences in θ of *c.* 5% were < 2 cm. Modeling an arid ecosystem with and without hydraulic lift,

Ryel *et al.* (2002) found differences in θ ranging up to 22%, but for short time periods. The use of root uptake compensation in the present model, which allows for water uptake from deeper soil layers when the uptake restriction factor for a given layer (i.e. URF(z)) is positive, most accurately represented the water drawdown in deeper layers under the treatment conditions; a result consistent with the theoretical arguments of Šimůnek & Hopmans (2009). Some of the water removed from these lower layers may well have been interned in a shallower layer before transpiring through the canopy, as demonstrated in a temperate coniferous forest (Domec *et al.*, 2010), but the timescale of VWC measures in this study does not capture these short-term processes.

Soil water limitations

How soil water limitations to gross or net primary productivity are simulated in these seasonally dry tropical rainforests has recently been a rich area of investigation (Lee *et al.*, 2005; Fisher *et al.*, 2007; Hutyra *et al.*, 2007; Ichii *et al.*, 2007; Saleska *et al.*, 2007). Many early GCMs that used 1-
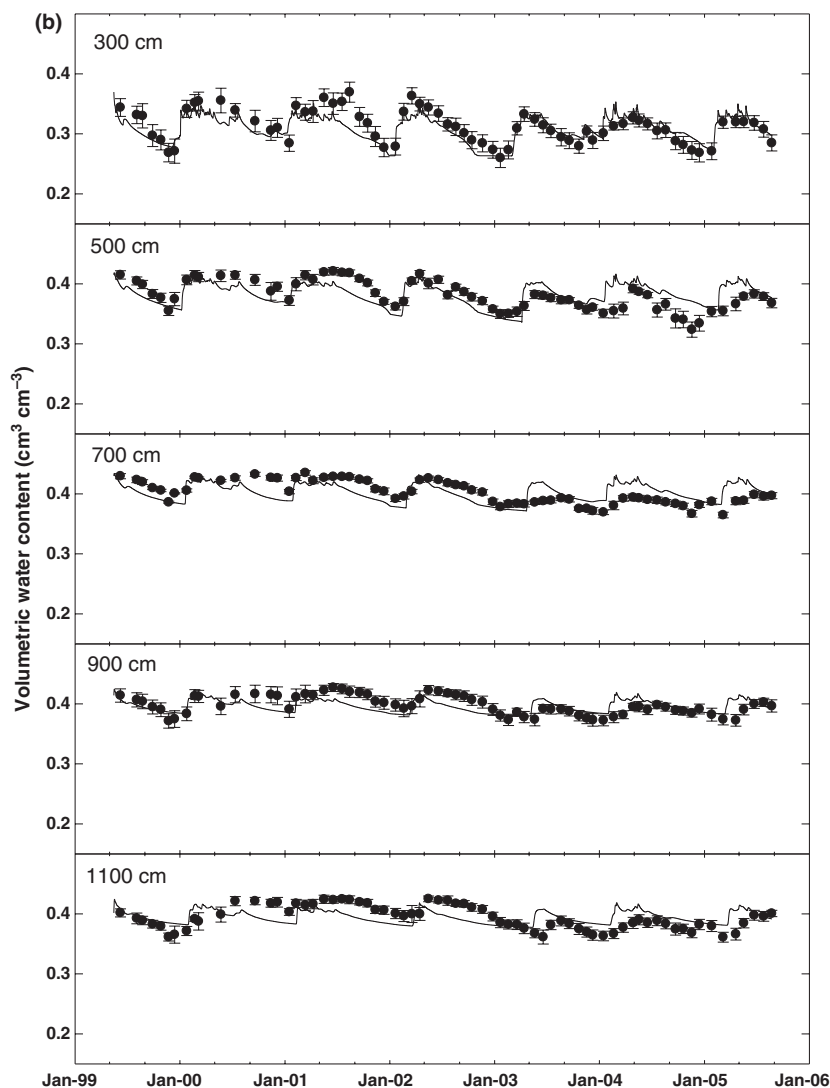
Fig. 4 (*Continued*).

or 3-m soil profiles presumed a seasonal water limitation to NPP. Currently, some empirical data (Hutyra *et al.*, 2007) and modeling studies (Baker *et al.*, 2008; Poulter *et al.*, 2009) suggest that for many seasonally dry areas within the Amazon basin no such limitation exists in most years. The canopy water flux data (i.e. measured AET) generated in close proximity to this study from an eddy-flux tower demonstrated that, in contrast to dry season water limitation, increases in AET during the dry season were observed relative to the wet season (Hutyra *et al.*, 2007). These AET data were used to drive soil water demand for the current simulations and, within the control plot, indicate a ready capacity for the soil profile through at least 5.5 m to provide sufficient water. On average the model estimate indicates that 58 ± 3, 73 ± 3, and 91 ± 1% of the water demand in the control plot was met by soil water from the upper 150, 250, and 550 cm of soil, respectively, which suggests that GCMs may have to incorporate a soil profile > 5 m to accurately assess water limitations. The model analyses of Ichii *et al.*

(2007), simulating GPP in the Amazon basin, were quite consistent with this conclusion. In areas of the basin with longer dry seasons, deeper soil profiles (going from 3 to 10 m) were required to sustain GPP (Ichii *et al.*, 2007). Utilization of hydraulic lift to supply sufficient soil water in GCMs, as done by Lee *et al.* (2005), is also possible but is still constrained by the availability of deep soil water for redistribution. Simply having deeply rooted soils with root water uptake compensation was sufficient in the present soil model to simulate VWC.

Of course, not all Amazonian soils are deep clay-rich Oxisols like those at the Tapajós exclusion experiment. Even in the Tapajós, Silver *et al.* (2000) found 0–10-cm clay contents to vary from 18 to 60%. In fact, it is estimated that Oxisols only cover 39% of the Amazon basin (Richter & Babbar, 1991) and soils within the Oxisol order may vary substantially. For example, at Caxiuanã soils are classified as an Oxisol (Latossolos amarelos in the Brazilian Classification) but possess only 9–20% clay in the upper
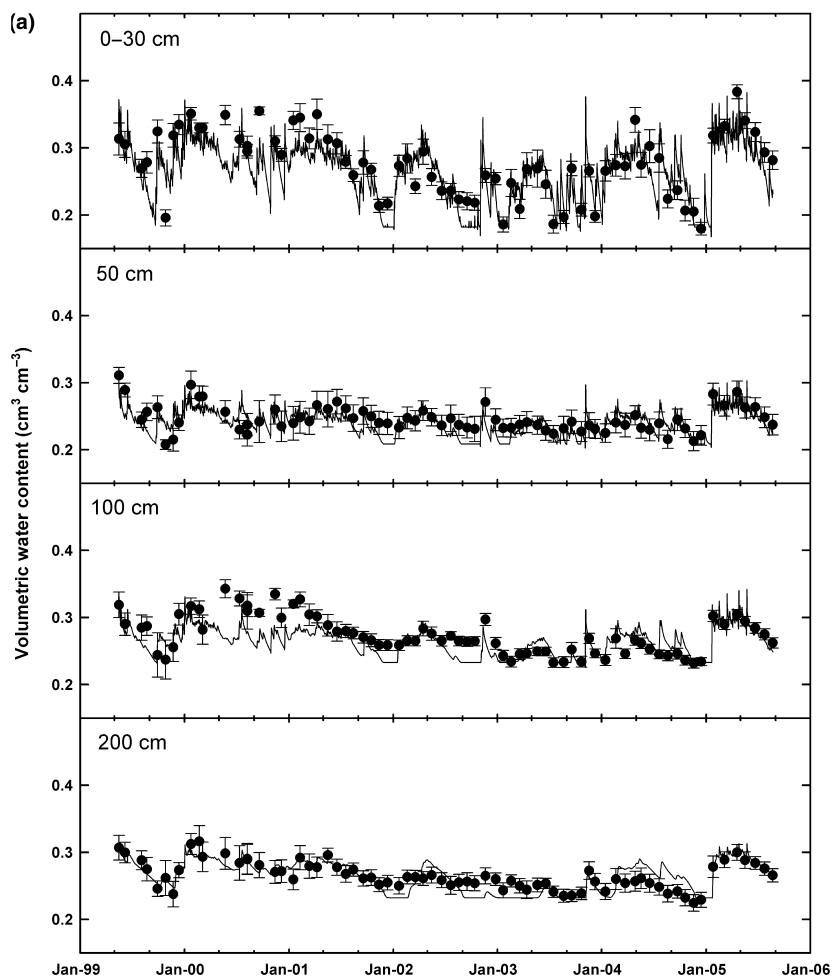
(a)

0–30 cm

50 cm

100 cm

200 cm

Volumetric water content (cm³ cm⁻³)

Jan-99   Jan-00   Jan-01   Jan-02   Jan-03   Jan-04   Jan-05   Jan-06

Fig. 5 Measured (circles; mean ± 1 SD) and simulated (line) volumetric water contents for (a) 0–200 cm and (b) 300–1100 cm under the treatment plot of the throughfall exclusion experiment in the Tapajo's National Forest, Brazil.

5 m (Ruvio *et al.*, 2007) while, in contrast, the Oxisols at Tapajós (Latossolos vermelhos) possess > 70% clay in all layers above 5 m. The critical role of soil rooting depth was previously demonstrated in a fire sensitivity model (Nepstad *et al.*, 2004). In this model a halving of soil rooting depth from 10 to 5 m doubled the area of Amazon forest that depleted soil to < 25% of the maximum plant available water, increasing its fire sensitivity. Clearly, conclusions about the role of deep root uptake will only be relevant were deep soil exists, but presently the ability to estimate these areas is limited.

Buffering by deep root uptake

Given the presence of deep soils, access to water reserves in these soils during drought may determine whether or not the tropical moist forests of Amazonia will be buffered from the deleterious effects of water deficits. The presence of roots at > 8 m in Amazonian Oxisols has been directly observed (Nepstad *et al.*, 1994) and in moist tropical forests on average has been estimated to exceed 7 m (Canadell *et al.*, 1996). The results from the Tapajós exclusion

experiment are consistent with an ability of roots in these moist forests to extract water from soil depths up to 11.5 m (Figs 4, 5). During the first 3 yr of the exclusion (2000–2002) and particularly in 2001 and 2002 plants were able to sustain AET by increasing the absolute volume of water taken up from the deepest portions of the profile (750–1150 cm). The percentage of modeled root water uptake contributed by these depths under exclusion increased from 3% in 1999 and 2000 to 6 and 12% in 2001 and 2002, respectively (Table 4). In 2003 and 2004, however, virtually no additional water was utilized from these soil depths, and this is also when significant tree mortality began to be observed (Nepstad *et al.*, 2007). During this study, it appeared that a contribution from deep soils of only *c.* 10% of water uptake was crucial for surviving dry periods.

In addition to increased mortality there was an observed decline in leaf area index of 21–26% in the exclusion plot from 2002 to 2005 and a decline in litterfall of 23% in 2003 and 10% in 2004 (Brando *et al.*, 2008). Direct measures of sap flux for 27 trees in each plot also indicated declines in water utilization of up to 73% on average in the dry season of 2003 (Cardinot, 2008). These declines in leaf
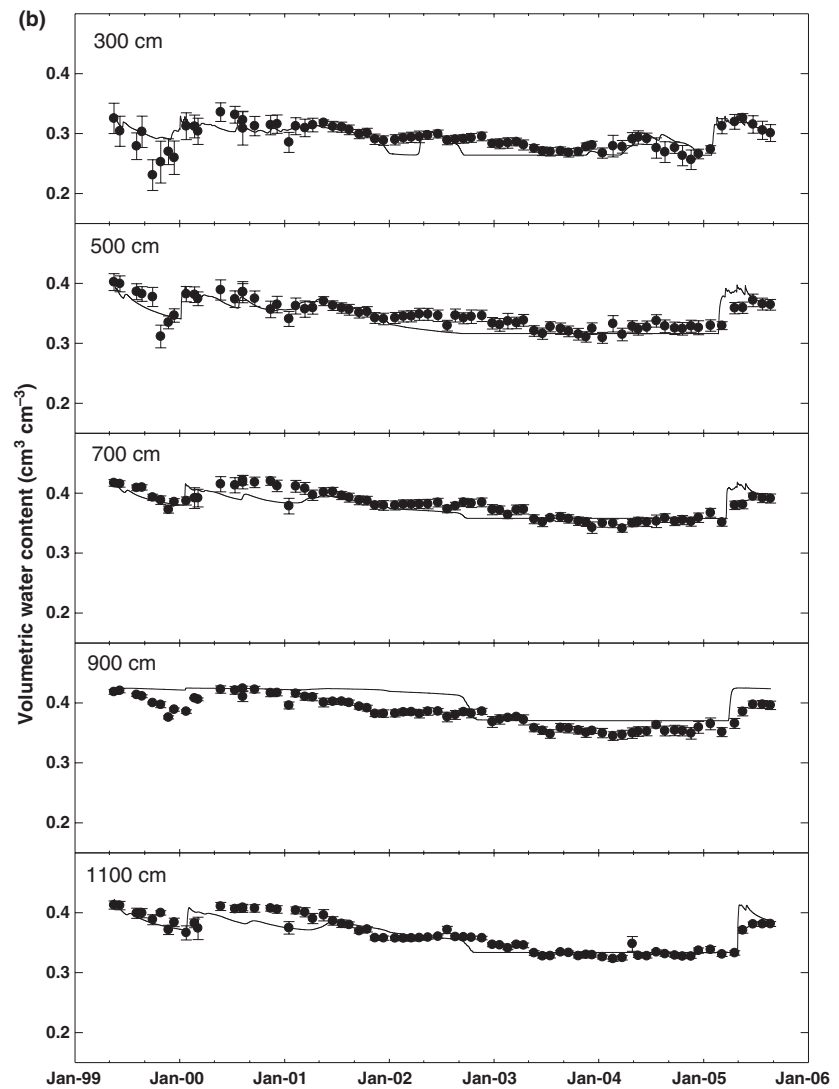
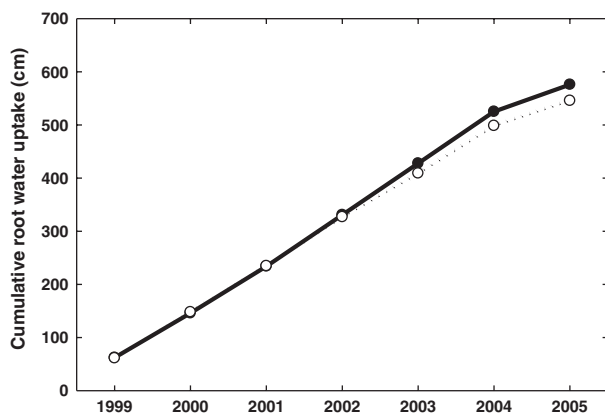**(b)**

Fig. 5 (*Continued*).

Fig. 6 Cumulative root water uptake under control (closed circles) and throughfall exclusion treatment (open circles) plots in the Tapajo's National Forest, Brazil.

area or sap flux were associated with a modeled decline in AET of 3, 12, 7, and 5% in 2002–2005, respectively. Clearly, there was some reduction in plant transpiration but, given the soil physical basis of the model and the fact that in the simulations PET as well as root biomass were kept constant, if water was available it would have been transpired. Thus, in the model, lack of deep soil water uptake in 2003 and 2004 was driven by soil moisture conditions and a lack of soil moisture recharge in 2003 and 2004. Despite this lack of recharge, however, VWC at depth was still > 0.32 cm^3 cm^{-3}. One interpretation is that soil waters are held at high matric potentials at these depths which resist root uptake.

Knowledge of the hydraulic properties of soils and parameters representing those properties (i.e. θ_r, θ_s, α, and n) is critical for estimating plant available water (PAW) in deeper soil depths, which is typically estimated as

Table 4 Annual root water uptake by soil layer as water depth (cm) and relative annual contribution (%) in control and throughfall exclusion plots in the Tapajo's National Forest estimated from a one-dimensional simulation model

Plot	Year	Layer													
		0–40	40–75	75–150	200	300	400	500	600	700	800	900	1000	1100	0–1150
Water depth (cm)															
Control	1999[1]	22.7	5.4	8.5	9.7	5.2	3.5	2.1	1.5	1.3	1.1	0.6	0.4	0.2	62.1
	2000	31.2	7.4	11.9	13.5	6.2	3.8	2.8	2.1	1.6	1.4	0.8	0.8	0.2	83.8
	2001	29.4	7.1	11.2	13.7	8.0	5.4	4.0	2.8	2.4	2.0	1.1	0.6	0.4	88.1
	2002	33.7	7.5	11.4	14.3	7.6	6.8	4.6	3.5	3.1	2.1	1.1	0.8	0.2	96.7
	2003	37.4	9.0	13.9	13.9	6.5	4.4	3.4	2.7	1.9	2.6	0.7	0.4	0.2	97.0
	2004	34.7	8.3	13.0	16.1	7.9	5.1	3.7	2.6	2.1	1.7	1.0	0.6	0.6	97.4
	2005[1]	18.6	4.8	6.5	7.5	4.3	2.6	1.8	1.3	1.5	0.9	0.6	0.3	0.1	50.8
Treatment	1999	22.4	5.3	8.2	9.5	4.9	3.6	2.0	1.5	1.1	0.9	0.7	0.8	0.5	61.3
	2000	30.5	7.3	11.4	12.8	6.5	4.2	2.9	2.2	1.7	1.3	1.2	1.1	0.8	83.6
	2001	28.4	6.7	10.8	13.5	8.1	5.1	3.7	2.8	2.3	1.8	1.3	1.4	1.0	86.9
	2002	35.1	7.4	10.8	9.9	5.1	3.9	2.0	1.6	2.0	3.8	4.4	3.4	2.8	92.2
	2003	50.8	12.0	12.4	5.8	0.9	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	82.0
	2004	40.7	9.7	14.2	14.0	7.7	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	89.6
	2005	19.0	4.6	6.4	7.0	3.6	1.7	1.3	1.0	0.7	0.6	0.3	0.5	0.3	47.1
Relative annual contribution (%)															
Control	1999	37	9	14	16	8	6	3	2	2	2	1	1	0	100
	2000	37	9	14	16	7	5	3	3	2	2	1	1	0	100
	2001	33	8	13	16	9	6	5	3	3	3	1	1	1	100
	2002	35	8	12	15	8	7	5	4	3	3	1	1	0	100
	2003	39	9	14	14	7	5	4	3	2	2	1	0	0	100
	2004	36	9	13	17	8	5	4	3	2	2	1	1	1	100
	2005	37	9	13	15	8	5	4	3	3	3	1	1	0	100
Treatment	1999	37	9	13	15	8	6	3	2	2	1	1	1	1	100
	2000	36	9	14	15	8	5	3	3	2	2	1	1	1	100
	2001	33	8	12	16	9	6	4	3	3	2	2	2	1	100
	2002	38	8	12	11	6	4	2	2	2	4	5	4	3	100
	2003	62	15	15	7	1	0	0	0	0	0	0	0	0	100
	2004	45	11	16	16	9	4	0	0	0	0	0	0	0	100
	2005	40	10	14	15	8	4	3	2	1	1	1	1	1	100

[1]1999 (May–December) and 2005 (January–May) were incomplete water years.

$$PAW = \theta_s - \theta_r \qquad \text{Eqn 6}$$

Previous research at this site described the sensitivity of the present hydrologic model to these parameters (Belk et al., 2007). Sensitivity to θ_s was greatest with water contents increasing by 50% for a twofold increase in θ_s, while a twofold change in θ_r elicited a 25% change in water contents. These values differ, however, in that θ_s is a 'physical' parameter that is well constrained by the dry bulk density and particle density of the soil. By contrast, θ_r is not well constrained by measurement and is usually obtained through a fitting procedure (Hodnett & Tomasella, 2002). It remains unclear what is the lowest matric potential that plants can achieve for water extraction, as it depends upon a number of factors, including root density and osmotic potential, soil texture and the capacity of plants to resist xylem embolism (Sperry et al., 1998). A permanent wilting point at −1.5 MPa is commonly an assumed default value

for this lower matric potential. Assuming the soil and leaves are in hydraulic equilibrium at pre-dawn, 'average' soil water potential may be inferred from pre-dawn leaf water potentials (Fisher et al., 2008). In the late dry season of 2002 and 2003, pre-dawn leaf water potential in the exclusion plot at Tapajôs were observed at −1.5 MPa (Nepstad et al., 2007).

Previously at this site calibrated θ_r values (c. 0.2 cm^3 cm^{-3}) were utilized that were lower than those determined analytically in the laboratory (c. 0.3 cm^3 cm^{-3}) or simulated in this study. This was done to achieve acceptable calibrations with VWC throughout the soil profile (Belk et al., 2007). Working in Paragominas, Brazil with a similar TDR network in deep soil pits, Jipp et al. (1998) also had trouble reconciling observed TDR values with laboratory-measured soil moisture retention curves, although in this location measured VWC was at times lower than VWC measured at −1.5 MPa in the laboratory. Fitted θ_r values exceeding 0.3 cm^3 cm^{-3}, which may indicate
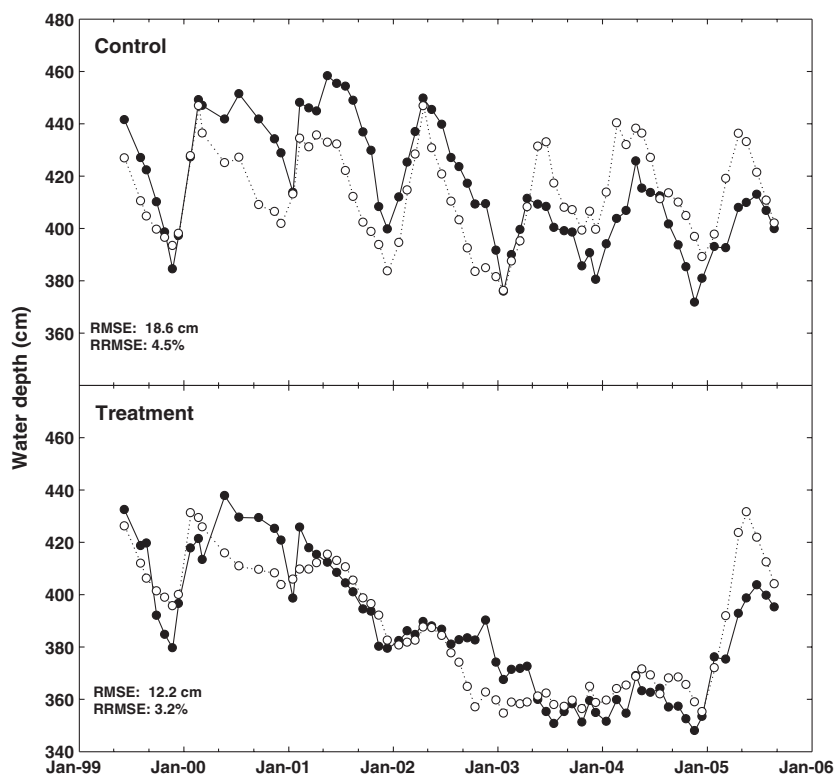
Fig. 7 Observed (closed circles) and predicted (open circles) water depth over the 0–1150-cm soil profile under the exclusion experiment in the Tapajos National Forest, Brazil. RMSE, root mean square error; RRMSE, relative root mean square error.

Table 5 Modeled water balance outputs for control and throughfall exclusion plots in the Tapajo's National Forest estimated from a one-dimensional simulation model

Year	Ppt	PET	ET from Interception	Control		Treatment	
				AET	Drainage	AET	Drainage
1999[1]	85.6	72.5	7.4	69.5	63.3	68.7	51.4
2000	248.1	104.1	19.8	103.6	135.6	103.4	48.0
2001	185.5	104.0	15.2	103.3	102.4	102.1	10.0
2002	190.4	112.1	15.4	112.1	72.4	107.6	0.6
2003	171.9	111.7	15.1	111.7	41.2	97.1	0.0
2004	220.8	113.7	15.9	113.3	110.1	105.5	0.0
2005[1]	162.0	68.7	10.5	61.3	71.9	57.6	43.2

All units are cm.
Ppt, precipitation; ET, evapotranspiration; PET, potential evapotranspiration; AET, actual evapotranspiration.
[1]Partial water year: 1999, May–December; 2005, January–August.

limitations to deep water uptake, were observed in 17% of 771 tropical soil profiles surveyed by Hodnett & Tomasella (2002).

High values of θ_r may be associated with limited deep soil water uptake, as suggested here, but the mechanism inducing this limitation is unclear. This physically based soil model emphasizes soil hydraulics rather than plant hydraulics, but both play a critical role (Sperry *et al.*, 2002) and the presumption that high soil moisture potential (Ψ_{soil}) exceeds suction potentials of plants (Ψ_{plant}) is only one possible mechanism available to limit deep soil water uptake.

For example, very low unsaturated hydraulic conductivity with increasingly negative Ψ_{soil} may result in loss of soil water conductivity in the rhizosphere between bulk soil and root surface, which could also limit water uptake (Newman, 1969). Similarly, cavitation in the root xylem may disrupt the cohesion–tension continuum and limit water uptake (Tyree & Sperry 1989), although some recent work suggests that the anatomical structure of deep roots may be well suited to minimize flow resistance and maximize deep water uptake (McElrone *et al.*, 2004).

Research in the Caxiuanã exclusion experiment very specifically addressed the critical nature of the soil-to-root hydraulic resistance to water uptake (Fisher *et al.*, 2007, 2008). The results obtained at Caxiuanã supported the idea that soil-to-root resistance exerted a strong control on transpiration relative to plant resistance (i.e. high-xylem resistance), particularly during the dry season. Under conditions of deep rooting as observed at Tapajôs, with a low density of fine-root biomass at depth and high θ_r, it is suggested that the soil-to-root resistance is critical in limiting deep root water uptake under extended drought.

Conclusion

Over the last 15 yr there has been a growing recognition that root water uptake in lowland tropical forests of the Amazon often extends to depths > 200 cm. Appropriately incorporating the mechanism of this root water uptake in

models of forest function is important for predicting effects of forest management or climate change. In the current study, a 6-yr record of volumetric water contents from a throughfall exclusion experiment was simulated under control and treatment conditions with a one-dimensional vertically integrated version of the Richards mass balance equation. The simulation with root uptake compensation through an 11.5-m soil profile accurately simulated the seasonal, annual, and exclusion dynamics. The success of this model suggests that other processes of hydraulic flow such as capillary rise or hydraulic root distribution may not move large volumes of water in this system. Furthermore, contributions of deep root water uptake are crucial, with the 250 to 550-cm layer contributing c. 20% of water demand under control conditions, while the deepest layers (550–1150) contributed c. 10%. Under the exclusion, root water uptake was sustained for the first 2 yr but declined thereafter. In years 3 (2001) and 4 (2002) of the exclusion experiment (i.e. the second and third years of the throughfall exclusion), deep root water uptake increased on both an absolute and a relative basis. This increase was not sustained, however, and these deep layers contributed zero root water uptake in 2003 and 2004 despite high VWC (i.e. > 0.30 cm^3 cm^{-3}). It appears that the capacity for deep root uptake of water is limited by changing soil-to-root resistance under severe drought, which may in part result from the high matric potential of water retention in these high-clay soils. Hence, the deep rooting habit provides an important adaptation to seasonal drought, but its buffering capacity is limited for longer term reductions in soil moisture.

Acknowledgements

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