

The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest

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[1] Moist tropical forests in Amazonia and elsewhere are subjected to increasingly severe drought episodes through the El Niño–Southern Oscillation (ENSO) and possibly through deforestation-driven reductions in rainfall. The effects of this trend on tropical forest canopy dynamics, emissions of greenhouse gases, and other ecological functions are potentially large but poorly understood. We established a throughfall exclusion experiment in an east-central Amazon forest (Tapajós National Forest, Brazil) to help understand these effects. After 1-year intercalibration period of two 1-ha forest plots, we installed plastic panels and wooden gutters in the understory of one of the plots, thereby excluding ~890 mm of throughfall during the exclusion period of 2000 (late January to early August) and ~680 mm thus far in the exclusion period of 2001 (early January to late May). Average daily throughfall reaching the soil during the exclusion period in 2000 was 4.9 and 8.3 mm in the treatment and control plots and was 4.8 and 8.1 mm in 2001, respectively. During the first exclusion period, surface soil water content (0–2 m) declined by ~100 mm, while deep soil water (2–11 m) was unaffected. During the second exclusion period, which began shortly after the dry season when soil water content was low, surface and deep soil water content declined by ~140 and 160 mm, respectively. Although this depletion of soil water provoked no detectable increase in leaf drought stress (i.e., no reduction in predawn leaf water potential), photosynthetic capacity declined for some species, the canopy thinned (greater canopy openness and lower leaf area index) during the second exclusion period, stem radial growth of trees <15 m tall declined, and fine litterfall declined in the treatment plot, as did tree fruiting. Aboveground net primary productivity (NPP) (stemwood increment and fine litter production) declined by one fourth, from 15.1 to 11.4 Mg ha⁻¹ yr⁻¹, in the treatment plot and decreased slightly, from 11.9 to 11.5 Mg ha⁻¹ yr⁻¹, in the control plot. Stem respiration varied seasonally and was correlated with stem radial growth but showed no treatment response. The fastest response to the throughfall exclusion, and the surface soil moisture deficits that it provoked, was found in the soil itself. The treatment reduced N₂O emissions and increased CH₄ consumption relative to the control plot, presumably in response to the improved soil aeration that is associated with soil drying. Our hypothesis that NO emissions would increase following exclusion was not supported. The conductivity and alkalinity of water percolating through the litter layer and through the mineral soil to a depth of 200 cm was higher in the treatment plot, perhaps because of the lower volume of water that was moving through these soil layers in this plot. Decomposition of the litter showed no difference between plots. In sum, the small soil water reductions provoked during the first 2 years of partial throughfall exclusion were sufficient to lower aboveground NPP, including the stemwood increment that determines the amount of carbon stored in the

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forest. These results suggest that the net accumulation of carbon in mature Amazon forests indicated by recent permanent plot and eddy covariance studies may be very sensitive to small reductions in rainfall. The soil water reductions were also sufficient to increase soil emissions of N_2O and to increase soil consumption of CH_4 —both radiatively important gases in the atmosphere. The possible reduction of tree reproductive activity points to potentially important effects of drought on the long-term species composition of Amazon forests. *INDEX TERMS*: 1615 Global Change: Biogeochemical processes (4805); 1655 Global Change: Water cycles (1836); *KEYWORDS*: biomass, NPP, tropical, ENSO, drought

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1. Introduction

[2] In recent years, the world's major moist tropical forests have experienced increasingly severe and prolonged droughts associated with the El Niño–Southern Oscillation (ENSO) [Trenberth and Hoar, 1997]. In 1997 and 1998, a particularly severe ENSO episode coincided with droughts that depleted soil moisture to more than 5 m depth in approximately one third of the closed-canopy forests of Amazonia (Figure 1), and desiccated tropical forests in Mexico and Southeast Asia, greatly increasing forest susceptibility to surface fires [Nepstad et al., 1999, 2001; Goldammer, 1999]. The frequency and severity of seasonal drought may increase in the future if ENSO is associated with global warming, as some statistical analyses suggest [Trenberth and Hoar, 1997], or if tropical deforestation provokes reductions in rainfall, as many models indicate [Costa and Foley, 2000; Lean et al., 1996; Nobre et al., 1991]. Tropical rainfall inhibition by smoke [Rosenfeld, 1999] may exacerbate this general drying trend in these moist tropical forest regions.

[3] The drying of moist tropical forests has important implications for their structure and functioning. Where drought exceeds the tolerance limits of tropical forest trees, mortality increases [Condit et al., 1995; Williamson et al., 2000]. Drought also triggers a positive feedback cycle of forest impoverishment in which increased drought-induced leaf shedding increases forest flammability and understory burning [Nepstad et al., 1999], causing tree mortality and even greater susceptibility to further burning [Cochrane et al., 1999; Nepstad et al., 1995, in press]. These forests maintain active leaf canopies during periods of prolonged drought by absorbing soil moisture stored to depths of 8 m and more [Nepstad et al., 1994; Jipp et al., 1998; Hodnett et al., 1996], and are therefore vulnerable to reductions in rainfall that would prevent the replenishment of deep soil moisture supplies. The potential effects of tropical forest drying on the global carbon cycle are large. In Amazonia alone, forest biomass (60–80 Pg [Houghton et al., 2000]) is equivalent to more than a decade of net human-induced carbon emissions worldwide.

[4] But before drought becomes severe enough to cause tree mortality or leaf shedding in moist tropical forests it may trigger several other important changes, including tree reproductive failure, reductions in stem and root growth, decreased forest floor decomposition, altered nutrient cycling, and changes in soil emissions of CO_2 , N_2O , NO , and CH_4 . In this paper, we report on the first 2.5 years of a throughfall exclusion experiment that we established in

east-central Amazonia (Figure 1). The first year of the experiment was devoted to pretreatment comparisons of two 1-ha forest plots. During the subsequent 1.5 years, we subjected one of the plots to partial exclusion (~60%) of throughfall for 7 months during the rainy season of 2000 and for 5 months during the rainy season of 2001.

[5] *Drought effects on moist tropical forests:* The leaf canopy regulates the flow of energy and water into and out of the forest, while canopy litter production is a critical component of the soil carbon budget, nutrient cycling and forest flammability. For this reason, much of our study focuses on canopy processes. When rainfall is less than evapotranspiration, soil moisture is gradually depleted, increasing tensions in the xylem sap that can eventually trigger stomatal closure and other physiological responses. One of the predicted responses of the forest to throughfall exclusion is canopy drought stress, including lower (more negative) leaf water potentials, reduced photosynthetic capacity, and increased leaf shedding.

[6] Many temporal patterns of leaf- and plant-level processes in moist tropical forests appear to be controlled by annual dry seasons, when evapotranspiration exceeds rainfall for several consecutive months. Trees reduce their leaf area during the dry season through leaf abscission, or renew their leaf crowns with more xerophytic leaves that are thicker (lower specific leaf area), higher in lignin, with lower photosynthetic light response, and lower concentrations of photosynthetic enzymes (and, hence, N and P) [Reich, 1995; Reich and Borchert, 1982; Borchert, 1994, 1998; Mulkey and Wright, 1996; Dias-Filho and Dawson, 1995; Nepstad et al., 1994; Niinemets et al., 1999]. But it has been difficult to identify the exact environmental cue of these seasonal changes, because solar radiation increases as rainfall decreases [Wright and Cornejo, 1990; Wright et al., 1999]. A throughfall exclusion experiment allows us to assess forest response to water stress independently.

[7] Flowering and fruiting are also strongly associated with the seasonal march of rainfall, with seed germination generally concentrated during the onset of the rainy season [Wright et al., 1999; van Schaik et al., 1993; Knowles and Parrotta, 1997; Curran et al., 1999]. A physiological link between drought (tree water stress) and reproductive events has been demonstrated for coffee [Alvim, 1960] and *Tabebuia* [Reich and Borchert, 1982], but remains to be examined for the vast majority of tropical trees and vines. We hypothesized that the initial stage of drought would stimulate the flowering of some tree species, but that this stress

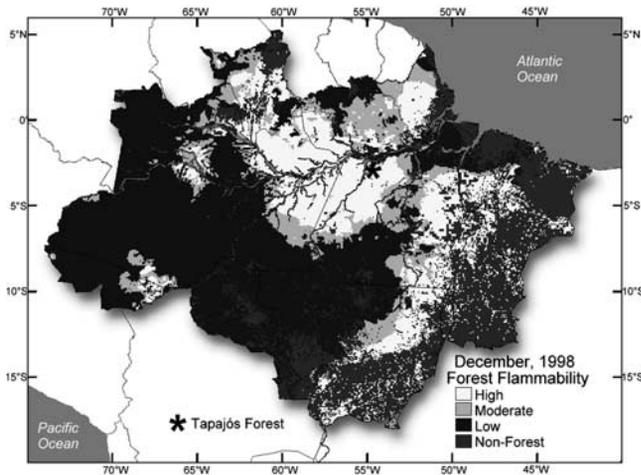


Figure 1. Map of the Brazilian Amazon showing the location of the Tapajós National Forest, where the throughfall exclusion experiment is established. This forest lies within the zone of high forest flammability that developed during the ENSO episode of 1998. Flammability ratings refer to the amount of plant-available soil moisture in the upper 10 m of soil at the peak of the 1998 dry season (following *Nepstad et al.* [1999, 2001]). “High” forest flammability indicates forest that depleted all PAW > 5 m depth.

would reduce reproductive success, with many fruits aborted before maturity.

[8] Little is known about the temporal variation of tree growth in the moist tropics because most of the tree species do not produce reliable annual growth rings [*Bormann and Berlyn*, 1981]. In the very wet and cloudy climate of La Selva, Costa Rica, where drought stress is very mild, variations in photosynthetically active radiation best explained interannual variation in stem growth [*Clark and Clark*, 1994]. Even mild drought at La Selva, however, was associated with reductions in stem diameter growth of some tree species [*Breitsprecher and Bethel*, 1990]. We hypothesized that stem diameter growth would be very sensitive to the onset of drought.

[9] Few studies have measured stem respiration for tropical forest trees. *Ryan et al.* [1994] measured stem respiration from two selected trees species in a Costa Rican forest and found that respiration was positively correlated with growth rate. Therefore, we expected respiration rates to decrease along with stem increment in response to throughfall exclusion.

[10] The response of root growth and mortality to drought is also poorly studied in moist tropical forests. On the one hand, soil drying can kill roots and inhibit root growth through the direct interaction between roots and soil [*Caldwell and Richards*, 1986]. On the other hand, many plants respond to drought by allocating a larger fraction of photosynthate to root production early in the dry season [e.g., *Dias-Filho*, 1995]. Soil respiration declined during the dry season in an eastern Amazon forest [*Trumbore et al.*, 1995; *Davidson et al.*, 2000b], indicating a net reduction in root and/or microbial respiration. We hypothesized that the initial effect of drought on roots would be an overall reduction in growth and associated soil respiration, despite an increase in root growth at depth.

[11] The net primary productivity (NPP) of moist tropical forests increases during the dry season as long as stored soil moisture is abundant, because of reduced cloudiness and greater PAR [*Oberbauer et al.*, 2000]. But NPP declines as drought-induced leaf shedding and stomatal closure begin [*Raich et al.*, 1991; *Tian et al.*, 1998; *Williams et al.*, 1998]. However, a dearth of data on stem increment, root growth and root respiration have prevented the quantification of seasonal patterns of NPP, and its allocation. We hypothesized that NPP would decline in the treatment plot relative to the control plot as drought stress increased, through reductions in stem growth and belowground production as predicted above. This reduction would be offset somewhat initially by an increase in litterfall.

[12] Reduced precipitation may have important feedback effects on climate change by altering soil emissions of radiatively important gases, such as CO₂, CH₄, N₂O [*Prather et al.*, 1995] and NO (NO is not, itself, a greenhouse gas, but it is a precursor to the formation of tropospheric ozone, which is a greenhouse gas [*Lammel and Graßl*, 1995]). Upland forest soils of the tropics are known to be important sources of N₂O [*Matson and Vitousek*, 1990] and NO [*Davidson and Kingerlee*, 1997] and sinks for CH₄ [*Potter et al.*, 1996]. Both primary productivity and respiration are high in many tropical ecosystems, resulting in large emissions of CO₂ from soils [*Davidson et al.*, 2000b]. The effects of land-use change and seasonal variation in precipitation on soil emissions of these gases have been studied [*Davidson et al.*, 2000a, 2000b; *Fearnside*, 1996; *Matson et al.*, 1990; *Stuedler et al.*, 1996; *Verchot et al.*, 1999, 2000], but the possible effects of long-term changes in rainfall have not been addressed.

[13] Trace gas emissions are affected by precipitation in at least two ways. First, soil water content affects soil aeration, which, in turn, affects microbial processes of production and consumption of these trace gases [*Davidson et al.*, 2000a; *Davidson and Schimel*, 1995]. We expected these effects to be manifested relatively rapidly, perhaps during the first year of the throughfall exclusion. Specifically, as these normally moist soils dried, we expected decreased emissions of CO₂ and N₂O, increased emissions of NO, and decreased net emissions or increased net consumption of atmospheric CH₄ from the treatment relative to the control soils. Second, reduced precipitation can also affect the availability of C and N substrates for soil microbial processes by altering root turnover, litterfall, decomposition, and mineralization [*Davidson et al.*, 2000a; *Davidson and Schimel*, 1995]. However, an increase in available N or C in the soil may first require a change in C allocation by plants, root mortality, or soil faunal activity. Hence, we hypothesized that these effects of drought stress on microbial substrate availability might not become apparent immediately, and we did not know how long it would take for these effects to be realized.

[14] Throughfall exclusion may also alter the biogeochemical flux of nutrients in the forest, particularly through its effects on the canopy and forest floor. The hypothesized increase in leaf shedding in response to drought would reduce canopy interception of incoming rainfall and the interaction of rainwaters with leaf surfaces. Fluxes of nutrients in throughfall from leaf washing or foliar leaching

would, therefore, be reduced. If the throughfall exclusion treatment also slowed the decomposition rate of leaves accumulating on the forest floor by reducing populations of soil fauna (mesofauna and macrofauna [Wheeler and Levings, 1988]) and decomposer microorganisms [Singer and Munns, 1987; Lavelle *et al.*, 1992], then the initial effects of the treatment may be an increase in forest floor retention of throughfall and a decreased return of mineralized nutrients to the mineral soil. The amount of water passing through the forest floor into the mineral soil would be greatly reduced (because of the treatment itself, and because of greater retention), as would the flux of nutrients cycling internally in the forest.

[15] In summary, we hypothesized that the initial stages of forest response to throughfall exclusion would include:

H1: a decrease in photosynthetic capacity and leaf water potentials;

H2: an increase in leaf shedding, resulting in greater litter production and reduced canopy cover;

H3: a decrease in rates of stem diameter growth, stem respiration and soil respiration;

H4: a decrease in total NO emissions, and an increase in the ratio of NO: N₂O emissions;

H5: an increase in soil consumption of atmospheric CH₄;

H6: lower canopy interception but greater forest floor interception of rainfall; higher concentration of solutes in litter leachate but decreased nutrient flux; and

H7: a decrease in litter decomposition rates.

2. Methods

2.1. General Approach

[16] Drought effects on forest processes were studied by comparing a 1-ha forest plot from which a portion of throughfall was excluded with a nearby 1-ha control plot. Each plot was partially isolated belowground from surrounding forest with a soil trench. Throughfall was partially excluded during the rainy seasons of 2000 and 2001 using plastic panels and wooden gutters installed in the understory. Canopy access was by wooden towers and catwalks. Deep soil processes were studied using shafts excavated to 12 m depth. Pretreatment plot differences were determined during a 1-year intercalibration period.

2.2. The Study System

[17] The experiment was located in Brazil's Tapajós National Forest, in east-central Amazonia (2.897°S, 54.952°W). This forest receives 600–3000 mm of rain each year, with a mean of 2000 mm; it experiences severe drought during El Niño events (Figure 1). The forest is situated on a flat terrace of Tertiary sediments capped by the Belterra Clay Formation [Clapperton, 1993], and is approximately 90 m above the water level of the Tapajós River, located 10 km to the west. The Oxisol soil (Haplus-tox) is dominated by kaolinite clay minerals and is free of hardpan or iron oxide concretions in the upper 12 m. This soil is similar to the clay soils described for a study site located in the same forest, and on the same Belterra Clay terrace, ~10 km from the throughfall exclusion experiment, where surface soil (0–10 cm depth) is 60% clay and 38% sand, bulk density is 1.02–1.23 (g cm⁻³), pH (H₂O) is 4.2, and total C is 4.2–4.3% [Silver *et al.*, 2000]. During well-

Table 1. Biomass, Basal Area, and Number of Tree and Liana Species in the 1-ha Throughfall Exclusion (Treatment) and Control Forest Plots, Tapajós National Forest^a

Parameter	Plot	
	Treatment	Control
Aboveground live biomass (>10 cm dbh trees, >5 cm dbh lianas), Mg ha ⁻¹	291	305
Basal area (>10 cm dbh), m ² ha ⁻¹	32.5	30.8
Coarse root biomass (>2 mm diameter, 0–12 m depth, n = 3), Mg ha ⁻¹	32.9 ± 6.8	30.0 ± 5.9
Fine roots, 0–0.1 m depth (<2 mm diameter, live and dead, n = 20), Mg ha ⁻¹	2.5 ± 0.25	3.5 ± 0.34
Fine roots, 0.1–6.1 m depth (<2 mm diameter, live and dead, n = 20), Mg ha ⁻¹	0.9 ± 0.08	0.7 ± 0.06
Total root biomass, Mg ha ⁻¹	36.3 ± 7	34.2 ± 6
Number of tree (>10 cm dbh) and liana (>5 dbh) species	182	203

^aMean ± SE for sampled variables.

drilling 6 km from the study site, the water table was encountered at ~100 m depth.

2.3. The Study Plots

[18] We selected two floristically and structurally similar, 1-ha (100 × 100 m) plots for the experiment from an initial survey of 20 ha of forest. We encountered 182 and 203 species represented by individuals with diameter at breast height (1.3 m dbh) of at least 10 cm (trees) and 5 cm (lianas) in the treatment and control plots, respectively (Table 1). The plots shared 54 tree species in common with at least 2 individuals per plot (and minimum diameter of 10 cm), and therefore allowed us to compare responses to the experimental treatment within the same species.

[19] The plots also had similar physiognomy, with the exception of a 600-m² treefall gap on the edge of the control plot. The forest surrounding the plots had emergent trees up to 55 m in height, with continuous canopy varying in height from 18 to 40 m. The study plots were placed in areas where most of the canopy was <30 m high to facilitate access to the tree crowns. 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, using the diameter-based allometric equations of Chambers *et al.* [2001] for trees and of Gerwing and Farias [2000] for lianas (Table 1). Coarse root biomass to 12 m depth (>2 mm diameter, live and dead) was 33 and 30 Mg ha⁻¹ for the treatment and control plots, respectively, based on roots encountered during the excavation of three soil shafts per plot (described below), and dried to 65°C (Table 1). Fine root biomass (0–2 mm diameter, live and dead) was 3.4 and 4.2 Mg ha⁻¹ for the treatment and control plots, respectively, based on twenty auger borings to 6 m depth, with 1.5-kg soil samples collected at 0–0.1, 0.5, 1 m, and at 1-m intervals to 6 m depth (Table 1). 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 following sieving.

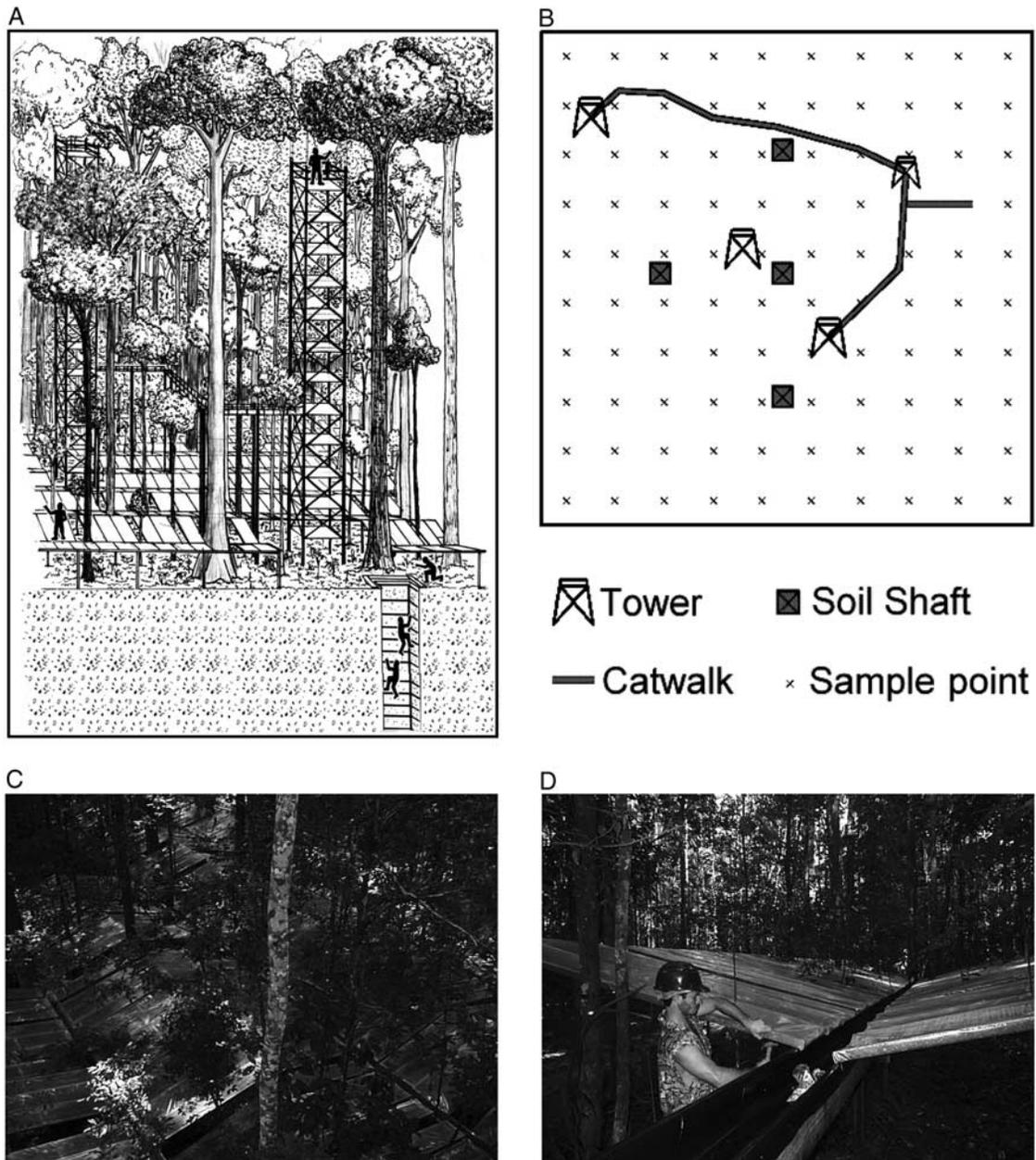


Figure 2. Side view (A), vertical view (B), and throughfall exclusion panels (C and D) of the throughfall exclusion experiment, Tapajós National Forest. Wooden towers (13–30 m) and catwalks provide access to the leaf canopy, while soil shafts (12 m) provide access to deep soil (A). (Data from only three shafts per plot were available for this paper.) A sampling grid provides permanent locations for measurements such as canopy openness (B). The throughfall exclusion panels drain into wooden gutters constructed in the forest understory (C and D).

[20] At their closest points, the plots were 25 m apart. Four wooden towers (13–30 m in height) and 80–100 m of catwalk (8–12 m height) provided access to the canopy in each of the 1-ha plots (Figure 2). Soil shafts (12-m deep, with 2.1×0.8 m openings, $n = 3$ per plot and $n = 5$ as of 9 April 2001), with a wooden infrastructure, provided belowground access. Sampling grids with 10-m distances between points were established with 10×10 points inside of each plot and a perimeter of sampling points outside of each plot, for a total of $12 \times 12 = 144$ points. These grids were used for measurements of surface soil water content, leaf area index, canopy openness, throughfall, litterfall, and

litter decomposition (Figure 2). Following initiation of the throughfall exclusion treatment, measurements of leaf area index, canopy openness, and litterfall in the treatment plot were made above the plastic panels, at points along the wooden drainage gutters, described below. This elevated sampling grid had $17 \times 6 = 102$ sampling points inside of the plot, with a spacing of 6 m between each gutter, and 16 m between each point along each gutter.

[21] A 1- to 1.7-m deep trench was excavated around the treatment plot to reduce the potential for lateral movement of soil water from the surrounding forest into the plot, and to provide a conduit for water excluded from the plot. A similar

trench was excavated around the control plot to avoid the confounding of throughfall exclusion and trenching effects. Forest parameters were compared at varying distances from the trench to assess trench effects on the forest.

[22] As with many large-scale ecosystem manipulations, this experiment was prohibitively large and expensive to permit replication (although a similar experiment is being established in eastern Amazonia under the leadership of P. Meir). Following the successful study design of large-scale ecosystem manipulation experiments, such as those at Hubbard Brook [Bormann and Likens, 1994], we have established a baseline for the two Amazon plots by taking an array of measurements in each plot during a ~ 1 -year intercalibration period beginning in November 1998, following trench excavation. This pretreatment calibration approach allows us to determine differences between the two plots before and after throughfall exclusion, facilitating rigorous testing of treatment effects.

2.4. Throughfall Exclusion

[23] Throughfall was partially excluded from the treatment plot during the rainy season of 2000, from late January to early August, and during the rainy season of 2001, from early January to late May, using 5660 panels made of clear, PAR-transmitting greenhouse plastic mounted on wooden frames (Figure 2). The panels were removed during the dry season to reduce their influence on the forest floor through shading and heating. Approximately $\sim 1\%$ of solar radiation penetrated the forest canopy of a similar Amazon forest [Nepstad *et al.*, 1996]. The panels increased forest floor temperature by no more than 0.3°C . 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. Each 3×0.5 m panel drained into a plastic-lined, wooden gutter (30 cm wide) that carried the water into the trench, which was also lined with plastic. The gutters served as catwalks for various measurements and panel maintenance. Water flowed by gravity from the perimeter trench into a deeper drainage ditch (1.7–2.3 m depth), which extended 220 m away from the plot into a small valley. The panels and gutters covered only $\sim 75\%$ of the forest floor, because we left openings around tree stems. We did not exclude stemflow from the plot, given its small contribution to forest floor soil water input (1–2% in other similar forests in Amazonia [Ubarana, 1996]), and its disproportionately high contribution to nutrient inputs to the soil. Estimates of daily rainfall were made with two wedge-shaped rain gauges located in the center of an 80-m-wide clearing 500 m from the experimental plots.

[24] Trampling of the forest floor was reduced in the experimental plots by directing foot traffic onto wooden walkways. Despite this precaution, 17% of the treatment plot and 15% of the control plot had visible signs of foot traffic as of January 2001 (based on three, randomly placed, 100-m transects across each plot). Forest floor damage in the treatment plot was greater than in the control plot because of the installation of panels and gutters. However, the control plot suffered similar forest floor damage because measurements of canopy cover, leaf area index, litterfall, and throughfall within the sampling grid required ground access; elevated drainage gutters provided access to the grid in the treatment plot.

[25] The success of this experiment depends, in part, upon knowledge of the lateral extent of the edge effect. To what extent were trees within the plot tapping soil moisture outside of the plot through lateral rooting below the trenches? Was soil moisture moving into the plot, driven laterally by gradients of water potential? We measured this edge effect through a deuterium pulse chase experiment (following Moreira *et al.* [2000] and described by Sternberg *et al.* [2000]), in which deuterium-labeled water was applied to soil plots outside of the trenches during the 1999 wet season. We found that the lateral distance of deuterium uptake by small trees was only 6 m; no label was detected in trees inside of the plots, and there was no evidence of lateral movement of deuterium in the soil [Sternberg *et al.*, in press]. On the other hand, our identification of roots encountered during excavation of the trenches indicates that some large trees (>60 cm dbh) have lateral rooting distances of >70 m (L. Lopes *et al.*, unpublished data, 2000). Hence, many of the large trees within the study plots may have suffered partial loss of their root system through trench excavation.

2.5. Measurements

2.5.1. Throughfall Exclusion

[26] We assessed the performance of the throughfall exclusion system by measuring water output from individual, randomly selected gutters during 17 rain events using five interconnected, 220-L drums. We also estimated water yield of the throughfall exclusion panels using a soil water balance approach, in which we compared the changes in total water content to 11 m depth in each of the plots for the exclusion periods. The amount of throughfall excluded by the panels was calculated for each exclusion period as the increase in soil water content in the control plot minus the increase in soil water content in the treatment plot, plus the difference between deep seepage of soil water (below 11 m depth) in the control and treatment plots. Deep seepage was estimated as evapotranspiration minus rainfall minus the increase in soil water content for a given time interval [Jipp *et al.*, 1998]. Evapotranspiration was assumed to be 4 mm d^{-1} , based on published estimates for Amazon forest (ET) during the wet season [Jipp *et al.*, 1998; Lean, 1996].

2.5.2. Soil Moisture

[27] Drought affects forests primarily through its effects on soil moisture. Our previous studies have found that forests in seasonally dry Amazonia absorb soil water from depths of 8 m and more during periods of severe drought [Nepstad *et al.*, 1994; Jipp *et al.*, 1998; Moreira *et al.*, 2000]. We therefore monitored volumetric soil water content (VWC) (cm^3 water cm^{-3} soil) to 11 m depth in both the treatment and control plots. We measured soil water using Time Domain Reflectometry (TDR), in which an electromagnetic wave is propagated along three, 30-cm, parallel, stainless steel rods imbedded in the soil to determine the soil's average dielectric moment (which is mostly a function of soil water content). The rods of each sensor were imbedded at one end in an epoxy resin head. Each sensor was installed at the end of a 1.5-m auger hole drilled horizontally into the wall of the shaft (the rods pushed into the intact soil) to avoid shaft effects on soil moisture; the holes were then back-filled with soil. Each of the shafts (three per plot until April 2001, when two additional shafts were plot were completed) had two

vertical sensors at the soil surface, and two horizontal sensors, in opposite walls, at 0.5, 1, 2 m, and at 1-m intervals to 11-m depth. In addition, two 25-cm TDR sensors were installed vertically next to each shaft, and 50-cm sensors at each of the 144 grid points in each plot; 100 of these grid points fell within the plot boundaries. VWC measurements were made using a cable tester (Tektronix 1502C) and the calibration equation developed in a similar Belterra clay formation, in eastern Amazonia [Jipp *et al.*, 1998]. TDR waveforms were recorded and analyzed using the WATTDR program (v3.11, Waterloo Centre of Groundwater Research, 1996). Each waveform was visually inspected for possible errors generated by the WATTDR algorithm.

2.5.3. Predawn Leaf Water Potential

[28] The predawn leaf water potential of mature trees was measured at approximately 2-week intervals during the dry seasons and at longer time intervals during the wet seasons to provide a measure of canopy drought stress. Six tree species common to both forest plots were studied, with three individuals per species in each plot, and four leaves sampled per individual. Leaves were clipped before sunrise, and stored in plastic bags on ice until water potential was measured using a Scholander pressure chamber (SoilMoisture 3005-1422 [Scholander *et al.*, 1965]). Measurements were always completed within one hour of clipping.

2.5.4. Litterfall

[29] Fine litter (leaves, reproductive parts, and twigs) was collected at 2-week intervals in $n = 25$ (through April 2000) and $n = 100$ (remainder of study period) 0.5-m^2 ($0.8 \times 0.62\text{-m}$) nylon screen collectors per plot, located at each of the sampling grid points within the plots. Twigs >1 cm diameter were excluded from the fine litter collectors, as in many previous measurements of fine litterfall in tropical forests [Vogt *et al.*, 1986]. Samples were dried at 65°C , and weighed. Reproductive parts (buds, flowers, fruits, and seeds) were separated manually, dried and weighed. The collectors were suspended at 0.1-m height initially, and were elevated above the plastic throughfall exclusion panels (1.5- to 3.5-m height) and to 1.5-m height in the control plot following panel installation. We also measured coarse litter production (twigs and stems $>1\text{-cm}$ diameter) using three 1×100 m transects in each plot. When panels were installed, coarse litterfall in the treatment plot was measured by collecting twigs and branches that fell on three 50×6 m sections of panel. This sample area was reduced by the area of the gaps that occurred between the panels, near tree stems.

2.5.5. LAI and Canopy Openness

[30] We measured leaf area index (LAI) before and during the throughfall exclusion treatment at each of the grid sampling points using two LiCor 2000 Plant Canopy Analyzers in differential mode [Welles, 1990; LI-COR, 1992]. One instrument was placed above the canopy on a wooden tower (Figure 2) to measure incoming radiation with no canopy influence; the other instrument was used for the understory measurement, made with the same directional orientation as the above-canopy instrument. The instruments were intercalibrated above the canopy at the beginning of each set of measurements. The light field of each sensor was reduced to 90° using opaque, 270° sensor caps. Measurements were made under conditions of diffuse skylight, usually before 0800 in the

morning or after 1700 in the afternoon. LAI calculations were made using the inner three quantum sensor rings to minimize the overlap among measurements made at adjacent grid points, and because this number of rings corresponded most closely with measurements calibrated in seasonally deciduous forests where LAI could be measured directly [Cutini *et al.*, 1998]. While this instrument does not distinguish between photosynthetic and nonphotosynthetic tissues, the latter component tends to be small, and it does provide a reliable relative measure of LAI for identifying treatment effects within the throughfall experiment.

[31] We also employed a spherical densiometer to provide a second, monthly measurement of canopy cover [Lemmon, 1956] at each of the grid points. In this method, canopy light gaps are visually quantified within a grid etched into a concave mirror. This measurement was made in each of the four cardinal directions, then averaged. One technician made all of the measurements to reduce observer error [Vales and Bunnell, 1988]. Both LAI and canopy openness were measured from the ground prior to panel installation. Following panel installation and continuing after seasonal panel removal, treatment plot measurements were made from the water collection gutters (Figure 2), 1–3 m above the ground.

2.5.6. Photosynthesis

[32] Photosynthetic light-response curves provide a measure of the photosynthetic properties of leaves, and are appropriate for determining the photosynthetic capacity of individual plants. We measured in situ light response curves on undamaged, mature leaves using an infrared gas analyzer with a temperature-controlled gas-exchange cuvette and an attached red LED light source (LI-6400, Li-Cor, Inc., Lincoln, NE). Each light response curve consisted of six incremental reductions in photosynthetically active photon flux density (PPFD), from 1700 to $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, at ambient CO_2 concentration. Leaves were allowed to equilibrate at each PPFD before measurement. Leaves were considered equilibrated if net photosynthetic rate was stable for at least 1 min. At least three measurements were taken per leaf at each PPFD level. Light response curves were typically completed within 20 min. Leaf temperatures averaged $31.3 \pm 0.11^\circ\text{C}$ in August and $29.38 \pm 0.11^\circ\text{C}$ in October (means \pm SE). All measurements were made between 0800 and 1500 h local time.

[33] Differences in light response curves due to throughfall exclusion were examined by comparing light-saturated photosynthetic rate (A_{max}) and apparent quantum yield (α). Values of α were estimated from the slope of the linear regression of photosynthesis versus incident PPFD below $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ [Dias-Filho, 1999]. A_{max} was determined from the curve plateaus. When appropriate, the estimated values were compared between treatments by two-sample t test, using the Dunn-Sidak adjustment to the probabilities.

[34] The shape of the average light response curves for each species were modeled by fitting data to a nonrectangular hyperbola (equation (1)):

$$A = \frac{\alpha * Q + A_{\text{max}} - \sqrt{(\alpha * Q + A_{\text{max}})^2 - 4 * \alpha * Q * k * A_{\text{max}}}}{2k} - R_d, \quad (1)$$

[Prioul and Chartier, 1977] or to equation (2):

$$A = A_{max} * (\tanh \alpha * Q / A_{max}) + R_d, \quad (2)$$

[Pattison *et al.*, 1998], where α is the apparent quantum yield of photosynthesis, Q is PPFD, A_{max} is the light-saturated rate of gross CO₂ assimilation, k is the curvature factor, R_d is leaf-level “dark” respiration, and A is photosynthetic rate. A nonlinear least squares curve-fitting procedure was used to estimate both models [StatSoft, Inc., 1997]. We employed the equation that provided the best fit to the data.

[35] In this paper, we present data for three species that occurred in both plots: *Licaria brasiliensis* (Nees) Kosterm. (Lauraceae, “louro”), a low canopy species, *Sclerolobium chrysophyllum* Poepp. (Fabaceae, “taxi vermelho”), a canopy species, and *Coussarea racemosa* A. Rich. (Rubiaceae, “caferana”), an understory species. Curves were measured for attached leaves at around 9, 20, and 7 m height, respectively, for one to two leaves per tree, and one tree per plot.

2.5.7. Flowering and Fruiting

[36] The reproductive phenology of each forest plot was monitored qualitatively through monthly visual observations of the crowns of all trees with boles ≥ 10 cm dbh ($n = 421$ and 501 in control and treatment plots, respectively). Trees were recorded as infertile, flowering, or fruiting based on crown inspection using binoculars.

2.5.8. Stem Growth

[37] Diameter increments of tree and liana stems (≥ 10 diameter) were measured using dendrometer bands that we fabricated using aluminum stripping (10-mm width) and stainless steel springs (Lee Spring Company, Brooklyn, NY [Cattelino *et al.*, 1986; Hall, 1944; Liming, 1957]). The bands were installed at breast height (1.3 m) or just above the swell of buttresses. The dendrometers were installed between January and March 1999, with measurements starting after a 3- to 5-month “settling” period. A total of 436 and 511 stems were banded in the treatment and control plots, respectively.

2.5.9. Stem Respiration

[38] Trees (and a few large vines) were selected from among those that had been equipped with dendrometer bands in both control ($n = 21$) and treatment ($n = 25$) plots. Small chambers (250–400 mL) were attached near the base of the tree using nylon straps. Closed-cell foam strips were glued along the rim of the chamber that made contact with the tree, and silicon sealant was added to create an airtight seal. Using an infrared gas analyzer (IRGA; LiCor 6252), closed-chamber measurements of the CO₂ increase rate were carried out for 1–2 min. Leaks were tested for by breathing along the chamber–tree interface at the end of each measurement. Measurements were carried out in February, April, June, and October 2000. We used correlation analysis to explore the relationship between stem respiration and growth.

2.5.10. Litter Decomposition

[39] We measured the rate of litter decomposition on the forest floor by placing screen bags containing leaf litter on the forest floor and removing a subset of the bags after 30, 60, 90, 150, 180 and 240 days. In each bag we placed approximately 10 g of mixed, oven-dried (65°C) leaves

collected from the plastic throughfall exclusion panels. To measure the effect of different litter fauna on decomposition rates, we employed three mesh sizes of plastic screening: large-mesh (2 cm), which excludes no litter fauna, intermediate mesh size (2 mm) which excludes macrofauna, and fine-mesh bags (< 0.125 mm), which exclude both mesofauna and macrofauna. A total of 360 litterbags were placed on the forest floor control and treatment plots (120 bags per plot for each mesh size) in September 1999. The bags were placed on small patches of mineral soil from which we had removed the litter layer. At each sample date, 20 bags were randomly selected, dried and reweighed to determine decompositional weight loss.

2.5.11. Soil Gases

[40] Fluxes of gases at the soil surface were measured using chamber techniques. Chambers consisted of a polyvinyl chloride (PVC) ring (20-cm diameter \times 10-cm height) and a vented PVC cover made from an end-cap of a 20-cm diameter PVC pipe. In September 1998, PVC rings were pushed into the soil to a depth of 2–3 cm to make the base of the chamber and have been left in place for the duration of the study. Six rings were placed in each of three subplots within the throughfall exclusion plot and the control plots, yielding a sample size of 18 for each treatment.

[41] A dynamic chamber method was used for measuring fluxes of NO [Verchot *et al.*, 1999] and CO₂ [Davidson *et al.*, 2000b]. Fluxes of N₂O and CH₄ were measured using a static chamber technique [Matson *et al.*, 1990; Verchot *et al.*, 1999, 2000] and using the same chamber bases as those described above. Syringe samples were analyzed in the laboratory by gas chromatography (GC) within 2 days of sampling. Diel effects have been found to be minor within a similar Amazonian forest, and detailed discussion of spatial and temporal variation using this sampling scheme have been addressed in other publications [Davidson *et al.*, 2000b; Verchot *et al.*, 1999, 2000].

2.5.12. Solution Chemistry

[42] Bulk precipitation inputs were collected with a 16-cm diameter funnel located above the canopy in each 1-ha plot. Throughfall collections were made using ten bottles with 16-cm diameter funnels located below the canopy in each plot. These ten bottles were randomly redistributed on the grid of permanent sampling points after every 2-week collection period. The funnels were supported above the throughfall exclusion panels and connected to the collection bottles with plastic tubing. Solutions passing through the forest litter layer were collected in three locations per hectare using PVC troughs of 30 \times 9 cm. In the exclusion plot litter leachate collectors were placed beneath openings in the panels. Tension lysimeters were installed at 25 and 200 cm in three soil pits running in a transect through each plot. During the pretreatment, intercalibration period Superquartz lysimeters (a mixture of quartz and Teflon, Prenat Equipment ApS, Copenhagen, Denmark) were installed. Due to the relatively low volume of water collected, preacid-washed ceramic cup lysimeters (SoilMoisture Equipment Corp, Goleta, CA) were also installed later in the study. Samples were collected from the field every two weeks. After collection, samples were taken to a laboratory in Santarém, and measured for conductivity, pH and

alkalinity [Clesceri *et al.*, 1998], filtered through 0.4 μm polycarbonate filters, and placed in cold storage for later chemical analysis. Analysis for NO_3 , NH_4 , PO_4 , K, Ca, Mg, SO_4 , Na, and Cl was performed by ion chromatography at the Centro de Energia Nuclear na Agricultura at the Universidade de São Paulo.

3. Results and Discussion

3.1. Water Input and Soil Water

[43] The plastic panels and gutters transferred an amount of water equivalent to $50 \pm 3\%$ (mean \pm SE) of rainfall into the plastic-lined trenches during the 17 rain events that were measured (Figure 3). Surprisingly, the rate of exclusion was not influenced by the total amount of rain for rain events up to 8 mm. Larger rain events exceeded the capacity of the water collection drums, and were therefore omitted from this analysis. Hence, we estimate that 890 mm of water were excluded from the treatment plot from 6 February to 7 August 2000, when rainfall was 1781 mm; 680 mm of water were excluded from 7 January to 31 May 2001, when rainfall was 1368 mm (Figure 4). Total throughfall (water captured by throughfall collectors divided by water captured by a pluviometer in a clearing, 500 m distant from the plots) was similar in control and treatment plots throughout the experiment. From 1 January 1999 until the initiation of the throughfall exclusion in late January 2000, throughfall was 81% (± 0.03) of rainfall in the control plot and 79% (± 0.03) in the treatment plot. During the subsequent 16 months, throughfall remained the same in both plots (80%). Hence, the exclusion system transferred approximately $\sim 60\%$ of throughfall during the posttreatment period when the panels were installed.

[44] Using water balance analysis (evapotranspiration = rainfall minus increases in soil water content minus deep soil seepage) for each exclusion period, we estimate that the panel and gutter system excluded 49% of rainfall, 816 and 643 mm in 2000 and 2001, respectively; this estimate is very similar to our estimate based on gutter output, assuming equal evapotranspiration between control and treatment plots during this period. This approach underestimates throughfall exclusion if soil water depletion and canopy water stress had already suppressed transpiration in the treatment plot. It appears that 50%, however, is a reasonable estimate of the amount of water that was diverted from the treatment plot expressed as a portion of rainfall.

[45] The effect of this throughfall exclusion on soil water content is determined by rainfall amounts. Annual rainfall during the experiment was 2240, 2700, and 1630 (through 30 June) in 1999, 2000, and 2001, respectively. Rainfall was abundant during both of the throughfall exclusion periods, averaging 9.7 and 9.5 mm d^{-1} in 2000 (late January to early August) and 2001 (early January to late May), respectively. Because daily evapotranspiration in Amazonian forests averages $\sim 4 \text{ mm d}^{-1}$ during the rainy season in Amazon forests [Jipp *et al.*, 1998; Lean, 1996], rainfall was, on average, sufficient to satisfy evapotranspirational water loss from the forest, even in the exclusion plot, where 50% of rainfall (60% of throughfall) was diverted from the soil. The exclusion treatment simulated a rainfall reduction from 9.7 and 9.5 mm d^{-1} down to 4.8 and 4.7 mm d^{-1} in 2000 and 2001, respectively.

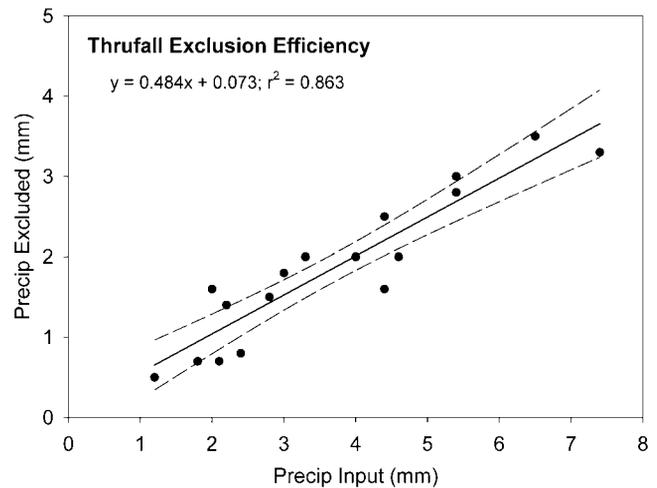
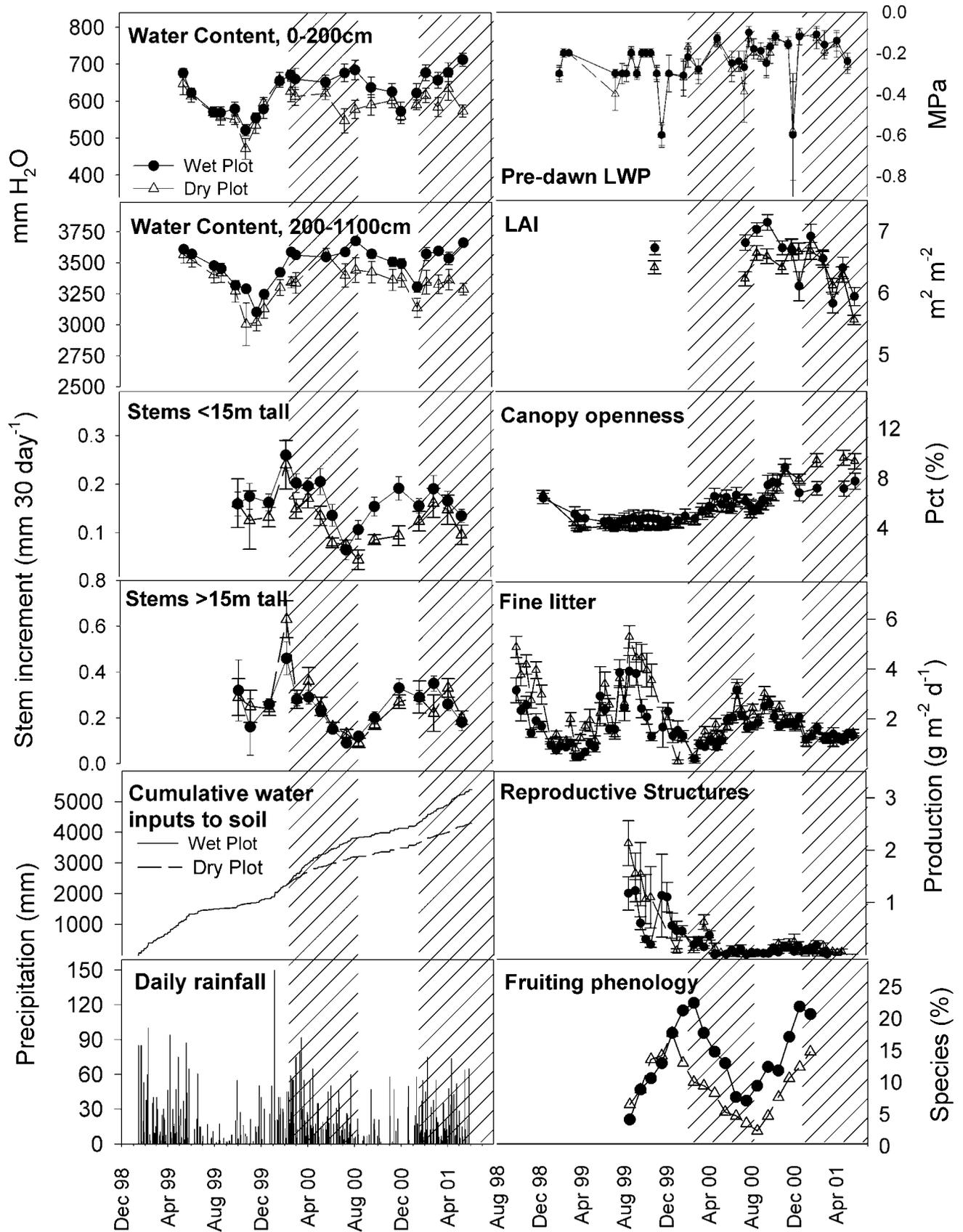


Figure 3. Throughfall exclusion amounts for 17 rain events (maximum rain amount of 8 mm). For each point, a rainfall event is plotted against the amount of throughfall that was excluded from the plot, measured by collecting the outflow from a single gutter-panel array ($5.8 \times 50 \text{ m}$) using five interconnected 250-L plastic drums. Rainfall events were measured in January and February 2000 and January, February, and March 2001. Linear regression (solid line) and 95% confidence interval (dashed line).

[46] Average daily rainfall was much higher during the 3 months prior to the 2000 exclusion period (7.7 mm d^{-1}) than during the 3-month period prior to exclusion in 2001 (3.1 mm d^{-1}). As a result, soil water content in the control plot increased in the upper 200 cm of soil relative to the treatment plot in 2000 by $\sim 100 \text{ mm}$, but showed little change from 200 to 1100 cm depth. The slight differences in deep soil water content between the two plots at the end of the 2000 exclusion period were already present prior to initiation of the exclusion (Figure 4). In contrast, the exclusion treatment prevented increases in soil water content of approximately 140 and 160 mm in 0–200 and 200–1100 cm depth intervals, respectively, during the second exclusion period (Figure 4). This larger treatment effect on soil water content during the 2001 exclusion period was (at least partly) the result of lower rainfall prior to initiation of the exclusion. Soil water content from 200 to 1100 cm depth was $\sim 200 \text{ mm}$ lower at the initiation of the 2001 exclusion compared to the end of this period (Figure 4). The exclusion treatment prevented the replenishment of this deep soil moisture. In contrast, deep soil moisture at the onset of the 2000 exclusion treatment had already been replenished. Soil moisture reduction during the 2001 exclusion period also took place during periods of low rainfall. Average daily water input to the soil in March 2001 was only 3 mm d^{-1} .

3.2. Leaf Water Potential

[47] The soil water reductions associated with the throughfall exclusion treatment were not sufficient to provoke substantial drought stress in the leaf canopy. Average predawn leaf water potentials (LWP_{pre}) were statistically indistinguishable between the two plots throughout the study period (Figure 4). As expected,



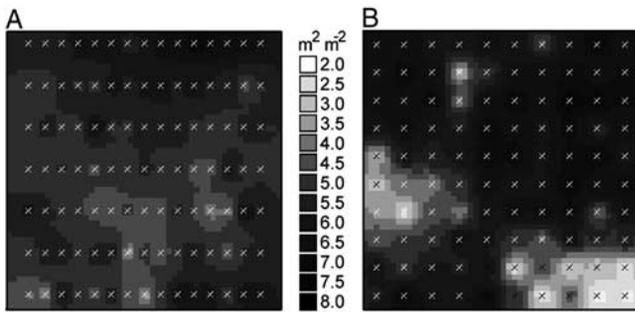


Figure 5. Spatial pattern of leaf area index in treatment (A) and control plots (B) of the throughfall exclusion experiment, May 2001, Tapajós National Forest. Treefall gaps, such as the one in the lower right corner of the control plot, were not included in calculations of the plot level means. (Black X's represent excluded points.)

LWP_{pre} dropped during periods of low rain, indicating higher tension in the xylem sap, but this decline was seen in both of the plots. The reductions in water content in both surface (0–200 cm) and deep (200–1100 cm) soil associated with the 2001 exclusion treatment may provoke reductions in LWP during the 2001 dry season, when soil moisture may be depleted to an even greater extent in the treatment plot.

3.3. Fine Litterfall

[48] Contrary to our predictions, fine litterfall appears to have decreased in response to throughfall exclusion (Figure 4). During the 1-year period prior to throughfall exclusion, litterfall averaged $0.6 \text{ g m}^{-2} \text{ d}^{-1}$ (34%) higher in the treatment plot than in the control plot, and was highly seasonal (Figure 4). Litterfall was 9.5 ± 1.1 and $6.6 \pm 0.8 \text{ Mg yr}^{-1}$ (mean \pm SE) in the treatment and control plots during the 12-month period leading up to the throughfall exclusion, and 6.3 ± 0.73 and $5.8 \pm 0.8 \text{ Mg yr}^{-1}$ following initiation of the exclusion treatment (February 2000 to May 2001). The difference in litterfall between the two plots disappeared after the exclusion panels were installed, perhaps in response to the surface soil moisture deficits that developed because of the throughfall exclusion treatment (Figure 4). Approximately one half of the reduction in fine litter production observed in the treatment plot was in the reproductive tissue component of litterfall. The production of flowers, fruits, and seeds was two times greater in the treatment plot prior to

throughfall exclusion, and this production declined sharply in both plots following initiation of the exclusion treatment (Figure 4, see below).

3.4. Canopy Cover

[49] Canopy openness increased and leaf area index (LAI) declined in both plots from the beginning to the end of the treatment period (May 2001) (Figure 4), indicating a thinning of the leaf canopy in both plots. Canopy openness doubled from a pretreatment average of 4% to 8–9% two years later, while LAI declined by $0.6\text{--}0.8 \text{ m}^2 \text{ m}^{-2}$ in each plot during the same period. Since rainfall was abundant during most of the experimental period, this canopy thinning may have been caused by root damage associated with excavation of the 1- to 1.7-m trenches around each of the plots in early 1999. Clearings associated with the mortality of two adult trees in the control plot (Figure 5) were excluded from these summaries of canopy openness and LAI, since we are interested in detecting drought-induced thinning of the intact canopy through leaf-shedding.

[50] Throughfall exclusion was associated with an increase in canopy openness in the treatment vs. control plot toward the end of the treatment period. A similar trend was found in the canopy gap fraction calculated from the LiCor 2000 data (not shown). The trend of LAI during the experiment was more variable. LAI was similar in treatment and control prior to exclusion (6.4 and 6.7, October 1999), and was lower in the treatment plot during the first year of exclusion (6.5 ± 0.1 and 6.8 ± 0.1 , respectively). This difference disappeared, however, during much of the subsequent period, with the treatment plot showing canopy thinning (6.2 ± 0.2 and 6.3 ± 0.2) during the last measurements of this sequence (Figures 4 and 5).

[51] In sum, the forest leaf canopy—which is responsible for regulating water and energy exchanges between the forest and the atmosphere, for determining the amount of solar radiation that enters the forest interior, and for controlling the rate and quality of organic matter deposited on the forest floor—exhibited a rather small response to the throughfall exclusion treatment during the first two exclusion periods, 17 months following initiation of the treatment. This may be a reflection of the capacity of Amazon forests that occur on deeply weathered clay substrates to avoid the effects of surface soil moisture deficits. When only the surface soil moisture supplies become depleted,

Figure 4. (opposite) Temporal trends in water, growth, and canopy parameters in treatment and control plots during the throughfall exclusion experiment, Tapajós National Forest. Periods of throughfall exclusion are indicated by diagonal hatching. Soil water content, integrated from 0 to 200 and from 200 to 1100 cm depth; means and standard errors for $n = 6$ sensors per depth in each plot. Stem radial growth increment of trees and lianas ≥ 10 cm diameter and <15 and >15 m height; means and standard errors for $n = 250$ and 205 stems <15 m and $n = 230$ and 200 stems >15 m in the control and treatment plots, respectively. Cumulative water input to the soil of the treatment and control plots (see text for calculations). Daily rainfall measured in a forest clearing 500 m from the study plots. Predawn leaf water potential of six tree species with $n = 3$ individuals per plot and $n = 4$ leaves per individual; means and standard errors. Leaf area index (LAI). Mean and standard error of $n = 100$ measurements made on the sampling grid (Figure 2). Sampling points ($n = 14$) influenced by treefalls in the control plot were omitted from the analysis. Canopy openness, measured using a spherical densiometer, in the treatment and control plots; means and standard errors (same protocol as for LAI). Fine litter production, excluding stems/twigs with diameter >1 cm; means and standard errors for $n = 25$ (through April 2000) and 100 points (remainder of period). Reproductive structures (flowers, fruits, and seeds) separated from fine litter samples. Finally, the percentage of all trees >10 cm dbh in each plot that were fruiting.

the forest can avoid drought-induced leaf shedding by absorbing soil moisture stored deeper in the soil, as has been documented in eastern and central Amazonia [Nepstad *et al.*, 1994; Jipp *et al.*, 1998; Hodnett *et al.*, 1996]. A previous attempt to experimentally manipulate drought-induced leaf shedding, on Barro Colorado Island, Panama (through dry season irrigation instead of wet season throughfall exclusion) also found no canopy response after a 4-month dry period [Wright and Cornejo, 1990], presumably because the forest canopy was controlled by deep soil moisture availability, which was unaffected by the experiment.

[52] Our hypothesis that drought-induced leaf shedding, leading to increased fine litter production and canopy thinning, would emerge as early forest responses to throughfall exclusion was not supported. Instead of increasing, fine litterfall declined, indicating a reduction in the rate of leaf production that was manifested as higher canopy openness and lower leaf area index only toward the end of the second period of throughfall exclusion.

3.5. Fruiting

[53] Tree reproductive phenology may have been more sensitive to the throughfall exclusion treatment than foliar phenology. Prior to the treatment, the percentage of tree species with flowering individuals (stem diameter ≥ 10 cm) was equal in the treatment and control plots. This percentage dropped in the treatment plot relative to the control plot and remained lower than the control for the remainder of the experiment (Figure 4). However, because this reversal began prior to the initiation of the exclusion treatment a cause and effect relationship appears equivocal. This phenological pattern, based upon direct observations of tree crowns, is similar to that observed for the mass of reproductive organs (buds, flowers and fruits) that fell into fine litter collectors. The production of reproductive organs was higher in the treatment plot prior to initiation of throughfall exclusion, and had already begun to decline prior to panel installation (Figure 4).

[54] The relationship between reproductive phenology and El Niño episodes has been described for Panama [Wright *et al.*, 1999] and Borneo [Curran *et al.*, 1999]; reproduction is often triggered by El Niño events, either in response to the drought or the increased solar radiation that accompanies these episodes. The reduction of fruiting that was observed in the treatment plot may have been maintained by small changes in LWP that were not detected by our plot-wide comparisons, and/or by internal (hormonal) communication between desiccating roots in the soil surface and tree crowns.

3.6. Photosynthetic Light Response Curves

[55] Few studies have described the influence of drought on the photosynthetic capacity of tropical forest trees in the field (for a review, see Mulkey and Wright [1996]). In our site, although some tree species studied showed no apparent response of photosynthetic capacity to the throughfall exclusion treatment, other species did. *Licaria brasiliensis* leaves exhibited similar light-saturated net photosynthesis (A_{max}) in both plots, but A_{max} was lower ($P < 0.01$) in the throughfall exclusion treatment during the peak of the 2000 dry season, in October (Figure 6). Similar evidence of a throughfall exclusion effect was found in the light response

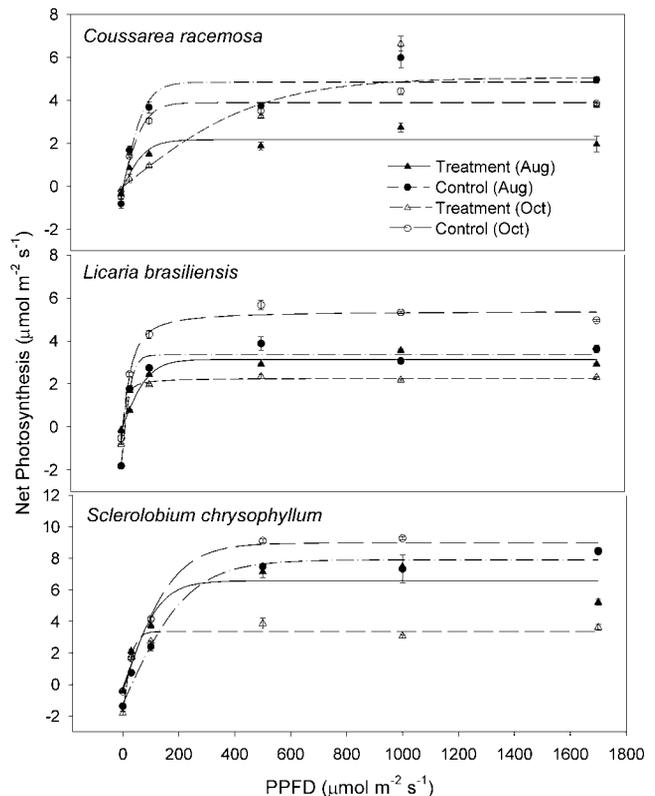


Figure 6. Photosynthetic light response curves for three tree species that occurred in both control and treatment plots of the throughfall exclusion experiment, Tapajós National Forest. Measurements were made on mature leaves ($n = 2$ per tree) early (August 2000) and late (October 2000) in the dry season; means and standard errors plotted along with the species specific regressions.

curves of *Sclerobium chrysophyllum*. In August, throughfall exclusion resulted in lower ($P < 0.01$) rates of A_{max} for *Coussarea racemosa*, but this pattern was reversed in October (Figure 6). A significant dry season effect in the reduction of net photosynthetic rate of some tropical saplings has recently been reported by Cao [2000] for a Bornean forest. For apparent quantum yield (α), no notable trends were observed. A similar lack of response of α to water stress has also been reported by Nilsen [1992], for the legume shrub *Spartium junceum*.

3.7. Stem Diameter Growth

[56] A decline in the radial growth of tree stems was observed during the dry season following the first throughfall exclusion period, when trees ≥ 10 cm dbh and < 15 m height exhibited a $\sim 20\%$ reduction in radial growth relative to pretreatment rates (Figure 4). The radial growth of larger trees (≥ 10 cm dbh and > 15 m height) did not respond to throughfall exclusion (Figure 4). Smaller trees may be more sensitive to the mild soil water deficits provoked by the throughfall exclusion treatment in the upper 2 m of soil because they tend to have shallower roots than large trees.

3.8. Coarse Litterfall

[57] The mass of twigs and branches (> 1 cm diameter) that fell to the forest floor each year was similar in each plot

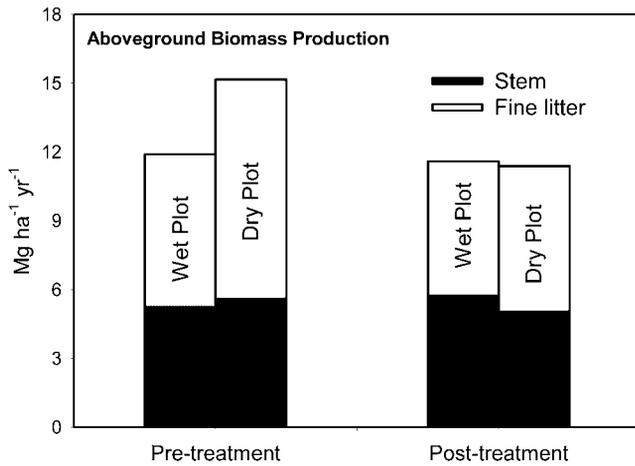


Figure 7. Annualized stemwood increment of trees and lianas (≥ 10 cm dbh) and fine litter production in wet (control) and dry (treatment) plots of the throughfall exclusion experiment, Tapajós National Forest. Data are summarized for the period prior to initiation of the throughfall exclusion (pretreatment, before January 2000) and following treatment initiation (posttreatment). The fine litter value includes foliage, twigs, fruits, and flowers.

before and after the initiation of throughfall exclusion. Coarse litterfall declined from 3.1 ± 1.6 to 0.9 ± 0.1 Mg ha⁻¹ yr⁻¹ in the treatment plot, but remained constant in the control plot (1.2 ± 0.2 Mg ha⁻¹ yr⁻¹ pretreatment and posttreatment.) Coarse litterfall was high prior to exclusion in the treatment plot because of a single, 51-kg branchfall event on one of the transects that, alone, represented 1.7 Mg ha⁻¹ yr⁻¹. (As of January 2001, we placed a 10-cm upper limit on the diameter of branches included in the coarse litterfall measurements. After this time, branches of >10 cm diameter were inventoried across the entire plot areas and are now included in a separate category.)

[58] Changes in coarse litterfall result from tree crown damage associated with storms, pathogens, drought stress and tree mortality, and cannot be attributed to changes in forest productivity on short timescales [Chambers *et al.*, 2001]. The similarity of coarse litterfall pretreatment vs. posttreatment indicates that there was little short-term tree damage caused by plot trenching (and severing of lateral roots), while the similarity of coarse litterfall between the two plots suggests that the throughfall exclusion experiment caused little measurable crown damage.

3.9. Aboveground Net Primary Productivity

[59] We employed the stem radial growth rates (Figure 4) to estimate the aboveground biomass increment of each plot using empirically derived allometric equations that describe tree and liana biomass as a function of stem diameter and height [Chambers *et al.*, 2000; Gerwing and Farias, 2000]. The aboveground biomass increment of trees and lianas ≥ 10 cm dbh was slightly higher in the treatment (5.7 Mg ha⁻¹ yr⁻¹) than in the control plot (5.3 Mg ha⁻¹ yr⁻¹) prior to the throughfall exclusion treatment, but declined relative to the control plot (5.1 vs. 5.8 Mg ha⁻¹ yr⁻¹) following initiation of the treatment (Figure 7). Hence, the reduction of radial stem growth associated with the throughfall

exclusion treatment (Figure 4) was manifested as a reduction of stem biomass accumulation at the plot level. When we add fine litterfall to the tree biomass increment, the overall pattern of reduced aboveground production in the treatment plot is further accentuated (Figure 7). The pretreatment production of stemwood and fine litter declined by one fourth, from 15.1 to 11.4 Mg ha⁻¹ yr⁻¹, in the treatment plot and decreased slightly, from 11.9 to 11.5 Mg ha⁻¹ yr⁻¹, in the control plot.

[60] The reduction in stemwood increment in response to small reductions in soil water content has important implications for the carbon balance of Amazon forests and, therefore, of the atmosphere. Permanent plot [Phillips *et al.*, 1998] and eddy covariance [Grace *et al.*, 1996] studies have provided evidence for substantial (~ 1 Mg ha⁻¹ yr⁻¹) net accumulation of carbon by mature Amazon forests. The results presented here indicate that this accumulation, if it is, in fact, taking place, is sensitive to moderate levels of drought, as suggested in the modeling experiment of Tian *et al.* [2000].

3.10. Stem Respiration

[61] Average stem respiration rates of individual tree species ($n = 4$ trees per species in each plot) varied by almost an order of magnitude, from 0.28 to 1.52 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and were lognormally distributed. We detected a statistically significant seasonal trend in mean monthly stem respiration rates using one-way ANOVA, with the lowest rates occurring during the peak of the 2000 dry season for both plots (October, Figure 8). There was no treatment effect, however. Stem respiration rates were significantly positively correlated with stem increment among the 18 species sampled in both plots ($r = 0.44$, $p < 0.000$).

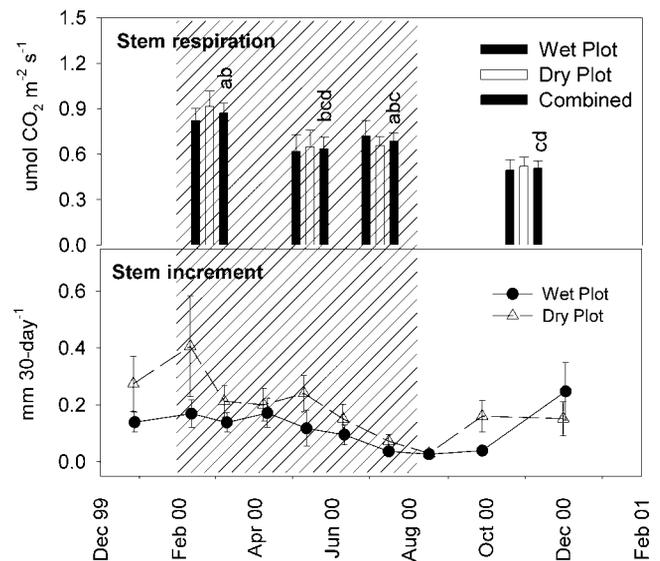


Figure 8. Average stem respiration rates and associated patterns of stem increment for control ($n = 21$), treatment ($n = 25$), and combined plots (only for stem respiration $n = 46$) during the first exclusion period in the throughfall exclusion experiment, Tapajós National Forest. Letters above plots refer to the combined sample; plots sharing the same letter are not statistically different (Tukey's studentized range test, $\alpha < 0.05$).

Respiration rates were also highly correlated with stem diameter ($r = 0.31$, $p < 0.000$). Although these data are preliminary, there appear to be seasonal changes in stem respiration, presumably brought about by reductions in stem wood production in drier months (Figure 8). However, despite the fact that 890 mm were excluded in 2000, there was no reduction in stem respiration in the treatment plot relative to the control plot during this first period of throughfall exclusion. Seasonal changes in stem wood production may be controlled in part by changes in leaf phenology, which had not yet begun in 2000.

3.11. Litter Decomposition

[62] Litter decomposition rates were similar between the two plots, showing little treatment effect. Only in the small mesh litterbags, which excluded litter mesofauna and macrofauna, did we find a temporary slowing of decomposition following initiation of the throughfall exclusion treatment, and even this effect disappeared by the subsequent sample date (Figure 9). Decomposition rates increased as a function of mesh size.

3.12. Soil Trace Gases

[63] The six dates of soil trace gas measurements made prior to initiation of the throughfall exclusion treatment revealed expected seasonal patterns that agree with previous observations from Amazonian forests [Davidson *et al.*, 2000b; Matson *et al.*, 1990; Steudler *et al.*, 1996; Verchot *et al.*, 1999, 2000]. Emissions of CO_2 and N_2O were usually higher during the rainy season than the dry season, whereas

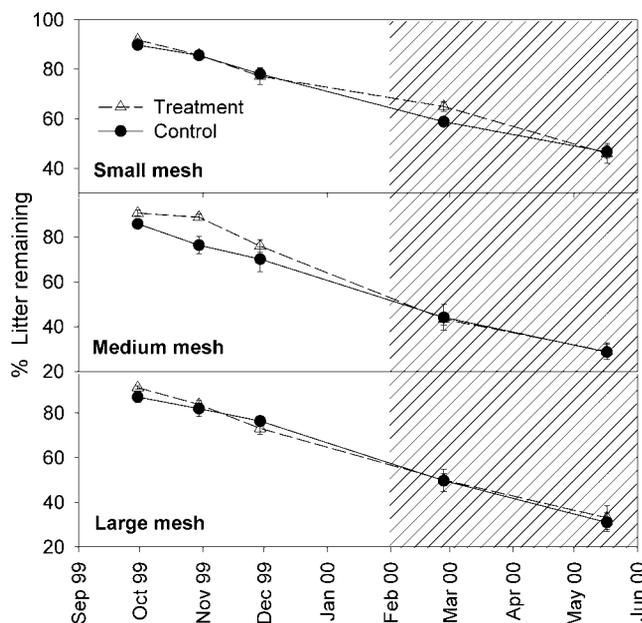


Figure 9. Rates of litter decomposition in control and treatment plots of the throughfall exclusion experiment, Tapajós National Forest. Litter samples were placed in screen bags with small (<0.125 mm), medium (2 mm), and large (20 mm) mesh openings to exclude different types of decomposer organisms. Means and standard errors for control and treatment plots over a period of 240 days during the first exclusion period.

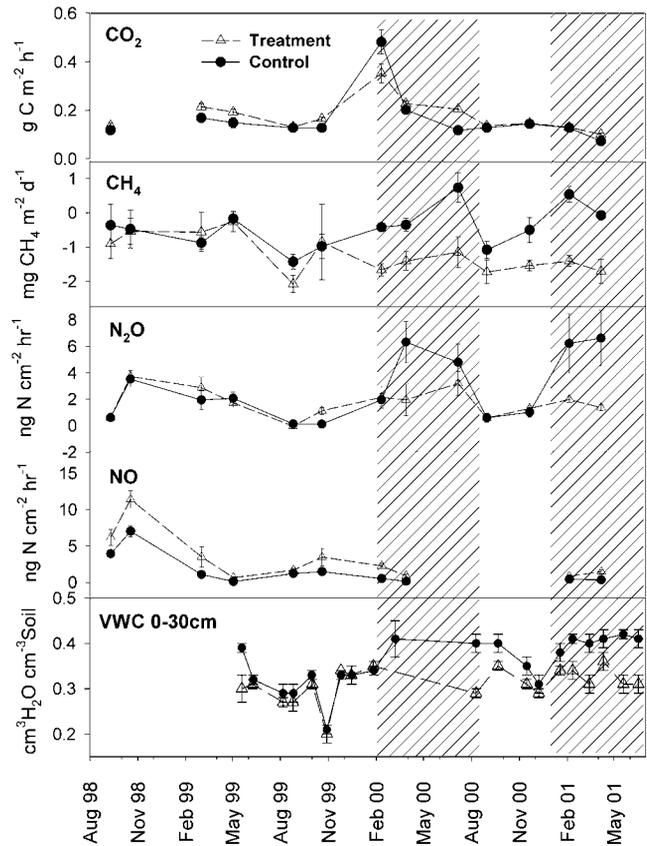


Figure 10. Fluxes of CO_2 , CH_4 , N_2O , and NO at the soil surface, and volumetric water content from 0 to 30 cm depth for the control and treatment plots of the throughfall exclusion experiment, Tapajós National Forest. Means and standard errors are based on measurements from $n = 18$ chambers per plot.

emissions of NO and net consumption of atmospheric CH_4 were greatest during the dry season (consumption is indicated by negative flux values) (Figure 10). There were no pretreatment differences between plots for CO_2 , N_2O , and CH_4 , but the treatment plot had consistently higher average emissions of NO . We do not know the source of this difference between plots in NO emissions. These results highlight the importance of an intercalibration period for distinguishing treatment effects from inherent plot-level differences.

[64] The abundant rainfall following the placement of the exclusion panels caused large increases in emissions of CO_2 and especially N_2O in February and March 2000 (Figure 10). These increases were larger in the control plot receiving natural throughfall compared to the exclusion plot, where only about 40% of the throughfall was allowed to reach the forest floor. This divergence between plots dissipated during the dry season in July, August, and November 2000 and reappeared during the rainy season of 2001. No effect of throughfall exclusion has been observed on NO emissions.

[65] Divergence between the two plots also occurred for CH_4 fluxes measured after the exclusion began. Consumption of atmospheric CH_4 declined (smaller negative values), during the 2000 wet season in the control plot, and net production of CH_4 was observed near the end of the wet

Table 2. Volume-Weighted Mean (± 1 SD) Concentrations for May 1999 to January 2000 from the Tapajós National Forest, Santarém, Brazil^a

Component		Precipitation ^b		Throughfall ^c		Litter leachate ^d				25 cm Tension ^e lysimeter			
				Dry Mean	Control Mean	Dry		Control		Dry		Control	
		Mean	SD			Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cond ^f	$\mu\text{S cm}^{-1}$	5.6	0.1	21	20	35	7.2	40	20.1	44	11	51	5
pH		4.9	0.1	5.64	5.62	5.81	0.31	5.72	0.24	4.46	0.21	4.82	0
Alk ^c	$\mu\text{eq L}^{-1}$	38	4	123	121	141	35	125	27	19	20	23	7
NO ₃	μM	2.5	1.5	15.2	12.4	117.9	10.3	163.5	151.6	315.8	186.1	437.9	ND ^d
NH ₄	μM	6.4	1.8	9.4	10.5	13.8	6	14.2	5.8	25.6	10.5	29.4	ND
PO ₄	μM	0.02	0.01	4.13	0.9	0.22	0.27	0.13	0.18	0	0	0	ND
K	μM	14.7	1.6	54.6	55.3	65.7	19.6	62.3	19.8	41.5	7.9	24.5	ND
Ca	μM	9.3	2.2	24.2	23.5	81	33.5	140.9	131.3	100.5	19	98.8	ND
Mg	μM	5.7	1	29.1	26.7	81.6	43.7	112.3	77.7	83.9	70.4	87.5	ND
SO ₄	μM	3.7	0	13.7	14.7	34.1	24.4	25.5	16.9	23.7	9.2	57	ND

^aStandard deviations represent spatial variation among samplers within the control and dry plot.

^bVWMs are estimated within each plot over 19 collection dates with $N = 1$ collector per plot. The mean represents the average for the site. A total of 144 cm of throughfall was collected during the period.

^c $N = 10$ collectors per plot that are randomly redistributed after every collection. VWMs are estimated within each collection with average volumes of the date then being used to estimate the annual VWM. A total of 118 cm of throughfall was collected during the period.

^dVWMs are estimated for each collector with $N = 3$ per plot. Means and standard deviations represent the spatial variability among the collectors. Sample collections ranged from 10 to 19 per collector.

^eVWMs are estimated for each collector with $N = 3$ per plot. Means and standard deviations represent the spatial variability among the collectors. Sample collections ranged from 1 to 3 per collector. In the control plot, only one sampler collected sufficient volumes for analysis by ion chromatography.

^fCond is conductivity and Alk is alkalinity estimated by endpoint titration to pH 4.5.

season. In contrast, CH₄ consumption remained at rates similar to dry-season pretreatment levels in the exclusion plot (Figure 10). This divergence persisted, but diminished, during the dry season of late 2000, and then reappeared during the 2001 exclusion period.

[66] For N₂O and CH₄, many of the short-term effects of throughfall exclusion have already been observed. Excluding throughfall prevented soil emissions of N₂O from increasing and consumption of atmospheric CH₄ from decreasing as would have naturally occurred during the wet season of 2000 and 2001. We expect a similar pattern in subsequent years, although new effects might also be observed as the impact of changes in substrate availability is manifest as chronic drought provokes root mortality and alters C allocation.

3.13. Solution Chemistry

[67] The volume-weighted mean (VWM) precipitation chemistry data from May 1999 to April 2000 indicates that these waters are quite pristine. Volume-weighted mean solution conductivity, $\sim 4 \mu\text{S cm}^{-1}$, and acid neutralizing capacity ($\sim 40 \mu\text{eq L}^{-1}$) are low, while pH is only mildly acidic, 5.2 (Table 2). Nutrient element concentrations are also low (Table 2) as are total inputs, for example, 2.8 and 0.04 kg ha⁻¹ for N and P, respectively. As these rainwaters pass through the forest canopy and the forest floor of both the control and treatment plots, conductivities increase indicating an increase in total dissolved solids in solution. These waters carry nutrients through the canopy and forest litter into the soil where concentrations are affected by exchange processes and biological activity. In surface soils, up to ~ 25 cm depth, these solutions continue to increase slightly in conductivity while pH decreases. This observed decrease in pH may result from the production of organic acids in this biologically active soil layer. The increasing concentration of NO₃ and NH₄ indicates that N mineraliza-

tion is an active process in this surface soil layer (Table 2). As water continues to descend through this upper portion of the soil profile, to a depth of ~ 200 cm, conductivities decrease while pH begins to rise (data not shown). During this intercalibration phase of the study differences in VWM solution concentrations between the control and dry plot were minimal.

[68] We hypothesized that early effects of our throughfall exclusion treatment on these patterns in solution chemistry should be most apparent in the composition of aboveground solutions such as throughfall or litter leachate. Soil solutions are potentially well buffered due to soil exchange processes as well as the retention of moisture belowground. We hypothesized that leaf shedding due to drought would diminish the interaction of solutions with foliar surfaces thus likely decreasing solution concentrations. Similarly, we hypothesized that in the short-term a decrease in forest floor decomposition rates would decrease the concentrations of litter leachate solution and thus the flux of nutrients into surface soils. We, in fact, did not observe any difference in throughfall concentrations between the treatment and control plots either pretreatment or posttreatment (Figure 11). Further, no differences have been observed for canopy interception of rainfall between the treatment plot either before or after the throughfall exclusion treatment, as explained above. The increase in canopy openness and decrease in LAI observed during the end of the 2001 exclusion period (Figure 5) were apparently not large enough to influence canopy interception.

[69] In contrast to throughfall solutions, differences in litter leachate solutions, collected immediately below the litter layer, were observed after the first year of throughfall exclusion. A statistically significant ($p < 0.01$) difference in solution conductivity, pH, and alkalinity was observed after this period (ANOVA with treatment and date as main effects for preexclusion and postexclusion solutions). Prior to

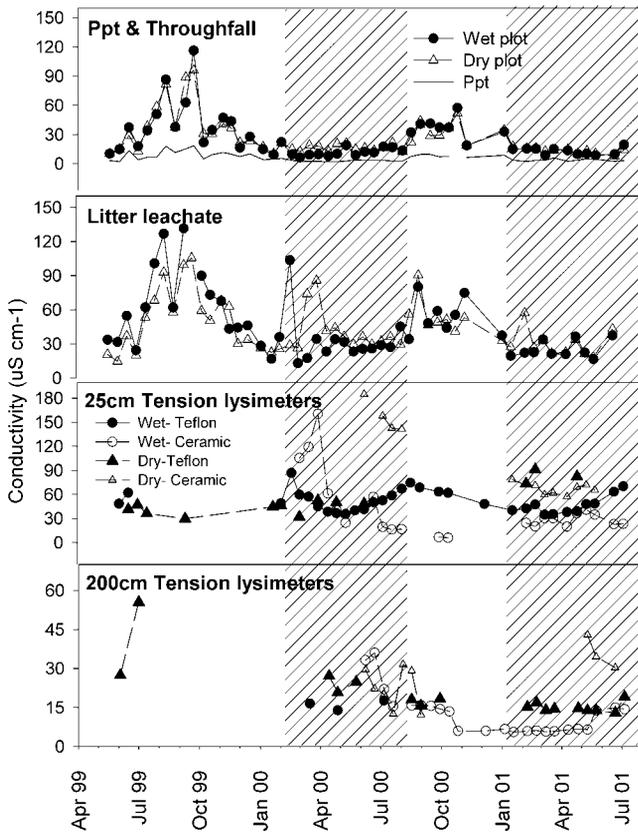


Figure 11. Conductivity of rainwater (above the canopy), litter leachate beneath the soil litter layer ($n = 3$), and soil water extracted with Teflon and ceramic tension lysimeters ($n = 3$) installed at 25 and 200 cm depth in the control and treatment plots of the throughfall exclusion experiment, Tapajós National Forest.

exclusion, differences in litter leachate pH, alkalinity, and conductivity were apparent but not statistically significant ($p > 0.05$). Concentration increases in alkalinity or conductivity may be due to a concentrating effect from a decreased volume of litter leachate waters, but this same effect was not observed for pH. Thus the observed changes likely result from a more complex combination of volume decreases together with changes in nutrient cycling process. Despite these increases in solution concentrations, total elemental flux of dissolved solids in litter leachate (concentration \times volume) has likely decreased due to a decreased volume flux in drier soils (Figure 4). Our water balance analysis estimates deep soil water seepage of 4.2 mm d^{-1} in 2000 and 2.7 mm d^{-1} in 2001 in the control, compared to zero in the treatment plot, assuming a daily evapotranspiration of 4 mm. These results from the throughfall exclusion are as yet not clearly indicating a large change in solution chemical concentrations in aboveground components, but effects in soil O horizons may be emerging.

[70] In the mineral soil at depths of 25 and 200 cm, measures of pretreatment and posttreatment conductivity, pH, and alkalinity also may indicate the beginning of a treatment response (Figure 11). At the 25 cm depth, after the second year of throughfall exclusion the conductivity of soil solution is higher in the treatment plot compared to the

control ($p < 0.01$). This difference is present when comparing Teflon or ceramic lysimeters (Figure 11). No such difference was apparent between Teflon lysimeters during the intercalibration period. At the 200 cm depth, conductivity of soil solution also appears elevated, although low sample numbers currently limit statistical validation. At neither depth, however, were changes in pH or alkalinity evident (data not shown). Again, concentration of solutions in a drier soil could elevate conductivities but pH and alkalinity would be expected to respond accordingly, which is not presently the case. Despite this increasing conductivity and thus increasing dissolved solids concentrations, elemental fluxes through the soils most likely will decrease as the flow of water decreases in the exclusion plot. Ecosystem responses to soil drying other than evapotranspiration, such as increased root mortality, could further augment nutrient concentrations in solution, however, and thus potentially buffer the absolute decrease in element flux due to decreased water flow.

4. Conclusions

[71] The forest in the 1-ha treatment plot responded to two periods of partial throughfall exclusion in important and, in part, unexpected ways. The forest leaf canopy proved to be quite tolerant of the soil moisture reduction provoked by throughfall exclusion. Instead of a pulse of leaf shedding, the exclusion treatment appears to have inhibited the formation of new leaves, leading to a decline in fine litter production and, eventually, a thinning of the leaf canopy. This thinning was not sufficient to reduce the amount of rainfall making its way through the canopy. Preliminary evidence suggests that another early response to throughfall exclusion may be a reduction in photosynthetic capacity. This reduction in photosynthetic capacity corresponds to a decline in stem radial growth rates of medium-sized trees, which has important implications for the forest carbon balance [Grace *et al.*, 1996] and for the prospect of forest management for timber production [Barreto *et al.*, 1998]. Although inconclusive, the apparent decline of fruiting in the treatment plot has important implications for the future plant and animal species composition of Amazon forests provided with declining amounts of rainfall. Processes controlled by the aeration of the surface layers of soil, which are strongly influenced by surface soil moisture content, were affected by the throughfall exclusion treatment. The rapid increase in soil emissions of N_2O , from the control plot following throughfall exclusion, and the sustained consumption of CH_4 , can both be explained on the basis of improved soil aeration, and could change in subsequent years of throughfall exclusion, as drought-induced root (and tree) mortality increases. These predicted increases in organic substrates would exacerbate the increases in solute concentration (conductivity) of litter and mineral soil leachate that already appeared in the treatment plot.

[72] Subsequent years of throughfall exclusion should allow us to identify the complex interactions between canopy foliar and reproductive dynamics, stem growth, soil processes, and nutrient fluxes as exclusion provokes progressively larger soil moisture deficits. Of particular interest is the level of drought stress at which leaf shedding renders

the forest vulnerable to fire, and at which drought-induced tree mortality begins.

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