

## MORTALITY OF LARGE TREES AND LIANAS FOLLOWING EXPERIMENTAL DROUGHT IN AN AMAZON FOREST

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**Abstract.** Severe drought episodes such as those associated with El Niño Southern Oscillation (ENSO) events influence large areas of tropical forest and may become more frequent in the future. One of the most important forest responses to severe drought is tree mortality, which alters forest structure, composition, carbon content, and flammability, and which varies widely. This study tests the hypothesis that tree mortality increases abruptly during drought episodes when plant-available soil water (PAW) declines below a critical minimum threshold. It also examines the effect of tree size, plant life form (palm, liana, tree) and potential canopy position (understory, midcanopy, overstory) on drought-induced plant mortality. A severe, four-year drought episode was simulated by excluding 60% of incoming throughfall during each wet season using plastic panels installed in the understory of a 1-ha forest treatment plot, while a 1-ha control plot received normal rainfall. After 3.2 years, the treatment resulted in a 38% increase in mortality rates across all stems >2 cm dbh. Mortality rates increased 4.5-fold among large trees (>30 cm dbh) and twofold among medium trees (10–30 cm dbh) in response to the treatment, whereas the smallest stems were less responsive. Recruitment rates did not compensate for the elevated mortality of larger-diameter stems in the treatment plot. Overall, lianas proved more susceptible to drought-induced mortality than trees or palms, and potential overstory tree species were more vulnerable than midcanopy and understory species. Large stems contributed to 90% of the pretreatment live aboveground biomass in both plots. Large-tree mortality resulting from the treatment generated 3.4 times more dead biomass than the control plot. The dramatic mortality response suggests significant, adverse impacts on the global carbon cycle if climatic changes follow current trends.

*Key words:* Amazon rain forest; biomass; Brazil; carbon flux; climate change; dead biomass; drought; El Niño; ENSO; forest mortality; lianas; tropical forest.

### INTRODUCTION

Severe episodic droughts change the structure and function of moist tropical forests in important ways. Supra-annual drought events such as those associated with El Niño Southern Oscillation (ENSO) episodes are sometimes accompanied by higher adult tree mortality (Leighton and Wirawan 1986, Condit et al. 1995, 2004, Kinnaird and O'Brien 1998, Nakagawa et al. 2000, Williamson et al. 2000, van Nieuwstadt and Sheil 2005), higher or lower seedling mortality (Engelbrecht et al. 2002, Condit et al. 2004, Edwards and Krockenberger 2006), mast fruiting of some tree species (Curran et al. 1999, Wright et al. 1999), reduced seed set in other tree species (Brando et al. 2006, Wright and Calderon 2006), and increased forest flammability (Woods 1989, Nepstad et al. 1999, 2004, Ray et al. 2005, van Nieuwstadt and Sheil 2005). Soil moisture depletion during severe drought can stimulate stomatal closure, a decline in leaf area (Nepstad et al. 1994), and a reduction in wood

production (Nepstad et al. 2002, 2004), perhaps suppressing net primary productivity on regional scales (Tian et al. 1998). Of these responses to severe drought episodes, the mortality of adult trees may be the most significant. Large trees determine the three-dimensional structure of the forest, the degree of coupling between the microclimate of the forest understory and leaf canopy, and contain more carbon than any other moist tropical forest pool (with the exception of soil carbon, much of which cycles on millennial time scales [Trumbore et al. 1995]). High tree crowns that maintain substantial leaf area during seasonal droughts cast deep shade, helping to keep air vapor pressure deficits low near the ground, and preventing the fine fuel layer from drying sufficiently to ignite when agricultural fires provide sources of ignition (Ray et al. 2005). In this context, drought-induced tree mortality can initiate a positive feedback loop in which increased drying of the forest interior enhances the likelihood of forest burning, and that burning kills more trees, further diminishing the protective shade of the high, dense leaf canopy (Nepstad et al. 1995, 2001, Cochrane et al. 1999). The drought-induced death of centuries-old trees may be registered in the structure and carbon exchange of moist tropical forests for decades,

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causing net outflux of carbon as large dead biomass pools (dead wood and vegetation) decompose (Saleska et al. 2003, Rice et al. 2004) or net uptake of carbon as growing trees outpace respiratory losses. Our ability to predict the future of moist tropical forests within scenarios of more frequent and intense episodic droughts (Trenberth and Hoar 1997, Foley et al. 2002, Cox et al. 2004, Meir et al. 2006) and the role of these forests in contributing to the fluxes of carbon dioxide and other greenhouse gases to the atmosphere is currently limited by the paucity of our knowledge of how tropical trees respond to severe drought.

Tropical forests in regions of little rainfall seasonality have exhibited the highest stand-level tree mortality following severe drought. Tree mortality recorded after severe drought episodes ranges from a high of 26% in a forest with aseasonal rainfall in East Kalimantan 21 months after the severe drought episode of the 1997/1998 ENSO event (trees >10 cm dbh [van Nieuwstadt and Sheil 2005]), to no mortality response in two of three seasonally dry forests studied in Panama following the same event (1–10 cm and >10 cm dbh [Condit et al. 2004]); dbh is diameter at breast height. Within this broad range of mortality responses, several intermediate tree mortality responses to ENSO episode droughts have been reported. Tree mortality in one of the Panama forests that exhibited no response in 1997/1998 increased 50% following the 1983 ENSO episode, from 2% to 3% (Condit et al. 1995). In the Central Amazon, which typically has a mild dry season, tree mortality increased slightly from 1.1%/yr pre-ENSO to 1.9%/yr following the 1997/1998 ENSO event (>10 cm dbh [Williamson et al. 2000]). In an aseasonal Sarawak forest, tree mortality climbed from 0.9% pre-ENSO to 6.4 and 4.3% during the 1997/1998 ENSO episode, with little variation across topography (>10 cm dbh [Nakagawa et al. 2000]). Tree mortality was 10% in aseasonal Sumatra following the 1997/1998 ENSO (Kinnaird and O'Brien 1998) and 14–24% following the 1983 ENSO in Kalimantan (Leighton and Wirawan 1986). In a study of the response of nine forests on Mount Kinabalu, Borneo (Sabah), tree mortality did not respond to the 1997/1998 ENSO episode on upland sites with nutrient-poor soils, but increased two- to sixfold on the other sites (Aiba and Kitayama 2002).

It is more difficult to discern patterns in the differential responses of plant types to severe drought. In Panama and East Kalimantan, large trees suffered higher mortality rates than juvenile saplings or shrubs following the 1983 and 1997/1998 ENSO episodes, respectively (Condit et al. 1995, van Nieuwstadt and Sheil 2005), whereas in Sarawak small trees died more than large trees (Nakagawa et al. 2000). In the Central Amazon, post-ENSO mortality was even across tree size and species (Williamson et al. 2000). Condit et al. (1995) found that gap-colonizing tree species were more vulnerable to drought-induced mortality than generalist species, but only in smaller size classes. In some cases,

individual taxa or morphological features were associated with significantly higher drought-induced mortality, such as dipterocarps in Sarawak (Nakagawa et al. 2000) and trees with low wood density in East Kalimantan (van Nieuwstadt and Sheil 2005).

One explanation for the considerable variation in response of tree mortality to severe drought episodes may be the effects of the drought on the amount of soil water that is available to plants at each site (plant-available soil water, PAW), and the ability of different plant types to access this soil water. None of the studies cited here present measurements of PAW, so it is currently impossible to examine the role of PAW in explaining this variation. With depletion of PAW in surface soil layers, shallow-rooted plants may die more rapidly than deeply rooting plants. As drought proceeds and deeper PAW is exhausted, the mortality of large trees (that tend to have deeper root systems) may exceed that of small trees, since tall tree crowns have greater exposure to sunlight and associated evaporative demand than the partially shaded plants growing in the understory. (Understory and midcanopy trees, in contrast, receive partial shade from overstory species.) Hence, tropical forest ecosystems may reach a critical minimum threshold in their response to drought; this threshold is defined by the rainfall history at which PAW is depleted throughout the rooting zone. The identification of such a threshold, if it exists, could become an important task in the development of vegetation models that predict the response of tropical vegetation to future climate scenarios, and would demand increasingly sophisticated knowledge of PAW (Nepstad et al. 2004, Hutyrá et al. 2005).

We established a large throughfall exclusion experiment in an east-central Amazon forest and monitored PAW to 11 m depth to simulate a severe four-year drought episode, testing the hypothesis that PAW depletion reaches a critical threshold beyond which large trees begin to die. Like tall trees, lianas are also exposed to high sunlight and evaporative demand, and may also exhibit a threshold response. By experimentally examining plant response to drought, we were able to separate the effects of soil moisture depletion from the effects of increasing solar radiation, factors that are often confounded during natural drought episodes. We addressed the following questions. (1) Is drought-induced mortality of medium and large trees associated with depletion of PAW beyond a critical threshold? (2) Is the mortality response dependent upon life form (trees, palms, and lianas)? (3) Is the mortality response dependent upon the potential canopy position of the individual (overstory, midcanopy, and understory)? And (4), how much live biomass is killed by severe drought?

## METHODS

### *Site description and study design*

The throughfall exclusion experiment is located in the Tapajós National Forest in the east-central Brazilian

Amazon (2°54'12" S, 54°57'12" W). The region receives an average annual rainfall of ~2000 mm, varying between 600 and 3000 mm/yr, and suffers severe drought stress during ENSO years. Soils are deeply weathered Oxisols (Haplustox), with no concretions or impeding layers in the upper 12 m. The water table is ~100 m below the soil surface. Beginning in late January 2000 through December 2004, ~60% of throughfall (equivalent to approximately half the rainfall) was excluded from the 1-ha treatment plot (dry plot, D) using a system of ~5660 plastic panels located in the forest understory during the wet seasons (see Nepstad et al. 2002 for a complete description of the study and site). Treatment effects were assessed relative to measurements collected from a similar 1-ha control plot (wet plot, W) located nearby. Trenches (1.0–1.7 m deep) were dug around the perimeters of both plots to inhibit root access to water from the surrounding area for the D plot, and to balance any damage to root systems in the case of the W plot.

#### *Plant-available water and leaf water potential*

We measured soil water in both plots monthly using time domain reflectometry (TDR) (Jipp et al. 1998). Six deep soil shafts were equipped with 13 pairs of 30 cm long TDR probes. One pair of probes per shaft was installed vertically at the soil surface. The remaining probes were installed horizontally into the walls of the shaft at depths of 0.5, 1, and 2 m, and thereafter at 1-m intervals to a depth of 11 m. Volumetric soil water contents (VWC) obtained from the TDR measurements were used to derive estimates of plant-available water (PAW) within the soil profile over time.

PAW for the entire soil profile (intervals from 0 to 200 cm and 200–1100 cm deep) was determined by setting the permanent wilting point (minimum PAW) equal to the average minimum VWC recorded at each measurement depth in the D plot. After establishing the minimum values of VWC, PAW was determined as the difference between the observed VWCs averaged across sensors for each month and the global minimum values. The final, derived PAW variable is expressed as a percentage of the maximum potential for this soil ( $\%PAW_{\max} = 100 \times [\text{VWC at field capacity} - \text{VWC at minimum measured value}]^{-1}$  for each depth), and is integrated over two depth intervals in the measured soil profile (0–2 m and 2–11 m deep).

We measured predawn leaf water potentials (LWP; leaf water potentials were always measured at this time) of six common understory and midcanopy tree species found in both plots, using a pressure chamber, beginning in January 2000. Three mature individuals per species were repeatedly measured in each plot by sampling four leaves per individual biweekly. These data were averaged across species in each plot at each date to provide an estimate of plant water stress for each area. We also calculated a water stress integral (WSI) for each plot (Myers 1988). This procedure involved accumulat-

ing, over time, deviations in LWP relative to the maximum observed value determined for each species, providing a long-term index of plant water stress:

$$WSI = \left| \sum_{i=0}^{i=t} (LWP_{i,i+1} - LWP_{\max})n \right| \quad (1)$$

where  $LWP_{\max}$  is the least negative value recorded for LWP over time, and  $n$  is the number of days in the interval. The daily values for WSI determined in each area were summed over the period of the study ( $t$ , in days). We determined additional drought stress provoked by the treatment as the difference in the WSI between the W and D plots over time. When expressed as the difference between plots over the long term, WSI is advantageously linked directly to LWP, providing a physiologically based estimate of the treatment's cumulative impact on plant water relations. The fact that LWP recovered during the wet season in the D plot even while  $\%PAW_{\max}$  continued to decline provides evidence of this association.

#### *Floristic surveys*

We completed an initial survey of stems  $\geq 1$  cm dbh in March 2000, including identification to species and measurement of diameter at breast height (dbh = 1.3 m). Diameters of highly irregular or buttressed stems were measured just above the irregularity. We remeasured all previously inventoried individuals  $\geq 2$  cm in August 2003, providing a census interval of 3.2 yr. Stems 1–2 cm dbh were remeasured in September 2003 in four 2-m<sup>2</sup> subplots within each 1-ha plot to provide an estimate of recruitment into the  $\geq 2$  cm dbh size class. In addition, we monitored all trees  $> 10$  cm dbh monthly to assess their condition (live vs. dead), and to measure their radial increment using steel dendrometer bands. Plants with their bases located within 5 m of the edge of the trench were excluded from these analyses to minimize the influence of root damage. Finally, we eliminated a 20-m<sup>2</sup> area in the W plot from the analyses because the pretreatment death and subsequent collapse of one large tree damaged surrounding trees. Effective sampling areas used in the study were 0.81 ha (D) and 0.77 ha (W).

#### *Categories of stems*

We categorized plants in the initial survey by size classes, life forms, and potential canopy positions for tree species. Four stem size classes were examined: 2.0–5.0, 5.1–10.0, 10.1–30.0, and  $> 30$  cm dbh. Three life forms were identified: trees, lianas, and palms. Trees were classified according to overstory, midcanopy, and understory, based on the species' potential canopy position at maturity (as described by Ribeiro et al. 1999). Tree species not found in the reference ( $n = 17$ ) were omitted from this part of the analysis.

#### *Mortality and recruitment rates*

Mortality was assessed as death or disappearance of previously tagged stems. Standing stems were considered

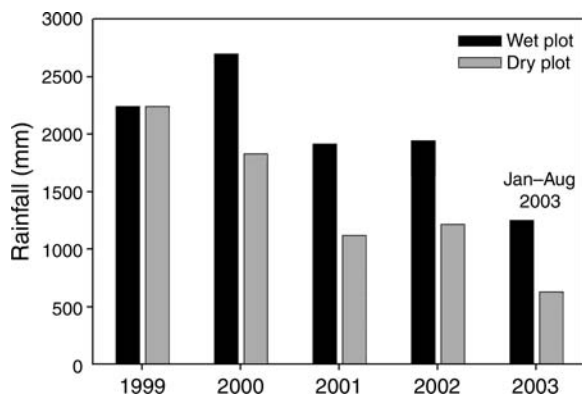


FIG. 1. Annual rainfall (measured in wet plot) and effective rainfall (rainfall minus water excluded by plastic panels; measured in dry plot) during 3.75 years of the throughfall exclusion experiment.

dead if their inner bark was dry and easily separated from the sapwood. The following equation was used to calculate annual mortality rates ( $m$ ):

$$m = [1 - (1 - S_D/N)^{1/t}] \quad (2)$$

where  $N$  is the initial number of stems,  $S_D$  is the number of dead stems at the end of the period, and  $t$  is the time interval between surveys measured in years (Sheil and May 1996).

Growth into larger diameter size classes was assessed by annual recruitment rates ( $r$ ) using

$$r = [(1 + X/N)^{1/t} - 1] \quad (3)$$

where  $X$  is the number of stems growing into a larger diameter class within the interval, and  $N$  and  $t$  are as defined following Eq. 2 (Nakagawa et al. 2000).

Survivorship within the two largest diameter size classes of trees (10–30 and >30 cm dbh) was determined on a monthly basis. Percent survival at each sample date is the ratio of the number of surviving stems to those present in the initial inventory. Recruited stems were omitted from this analysis.

The scientific name, number of individuals, and number of deaths of each species in this study is summarized in the Appendix.

#### Biomass calculations

We estimated the aboveground biomass of all measured plants using the following allometric equations: (1) moist forest equation presented by Chambers et al. (2001) for trees  $\geq 5$  cm dbh; (2) primary forest equation of Nascimento and Laurance (2002) for trees 2–5 cm dbh; (3) the equation of Gerwing and Farias (2000) for woody lianas; and (4) the equation presented by Hughes et al. (1999) for stemmed palms. Biomass values were converted to carbon equivalents by multiplying dry mass values by 0.5.

#### Statistical tests

We used a  $2 \times 2$  contingency table analysis to assess differences in mortality between plots. Initial stem counts and the number of dead individuals at the end of the census interval within each plot provided the cell values. Hypothesis tests were carried out using one-tailed probabilities based on Fisher's exact test ( $H_a$ : mortality in the treatment plot has increased due to the drought). This procedure was followed for each of the 10 plant categories. Binomial probabilities were used to estimate 95% CI of the annual mortality rates determined for each plant category.

## RESULTS

### Water balance

The experiment excluded  $\sim 60\%$  of throughfall from the soil when the panels were in place; a total of 620–890 mm of throughfall was excluded on an annual basis. We therefore induced an effective annual rainfall of 1810, 1120, and 1130 mm in 2000–2002 and 630 mm during the first eight months of 2003 (Fig. 1). Since 2000 rainfall was above average (2700 mm), effective rainfall during year 1 of the experiment was similar to the average for the site. In 2001 and 2002, effective rainfall was higher than total rainfall during the 1998 ENSO episode, when the site received only 630 mm of rainfall. In sum, the rainfall regime simulated during the study period was similar to rainfall during a moderate to severe ENSO event, with the important difference that the low level of effective rainfall was maintained for nearly three years.

In the upper 2 m of the soil profile PAW was reduced to 41% of  $PAW_{max}$  in the D plot, while the W plot remained at 83%  $PAW_{max}$  after the second wet season (January–July 2001) (Fig. 2b). Deep soil water underwent a similar pattern of depletion during this period in the D plot. Within 2–11 m of the soil profile, soil water dropped to 47% and 87%  $PAW_{max}$  in the D and W plots, respectively (Fig. 2c). After the second season of throughfall exclusion, drought stress also impacted canopy water status, inducing a 0.66 MPa difference in LWP between the two plots (Fig. 2a). During the fourth exclusion period, soil water in the D plot declined to 14% and 3%  $PAW_{max}$  within the 0–2 m and 2–11 m profiles, respectively. The corresponding values of % $PAW_{max}$  for the W plot were uncommonly low, 58% and 43% in August 2003, reflecting incomplete wet season recharge of soil water following the unusually strong dry season in 2002 (Fig. 2d). Following four seasons of throughfall exclusion, the normal pattern of soil water recharge and depletion, discernible in the W plot, became indistinguishable in the D plot (Fig. 2).

### Drought-induced changes in stem recruitment and mortality rates

Stem distributions by size class were similar for both plots in March 2000 when the initial inventory was

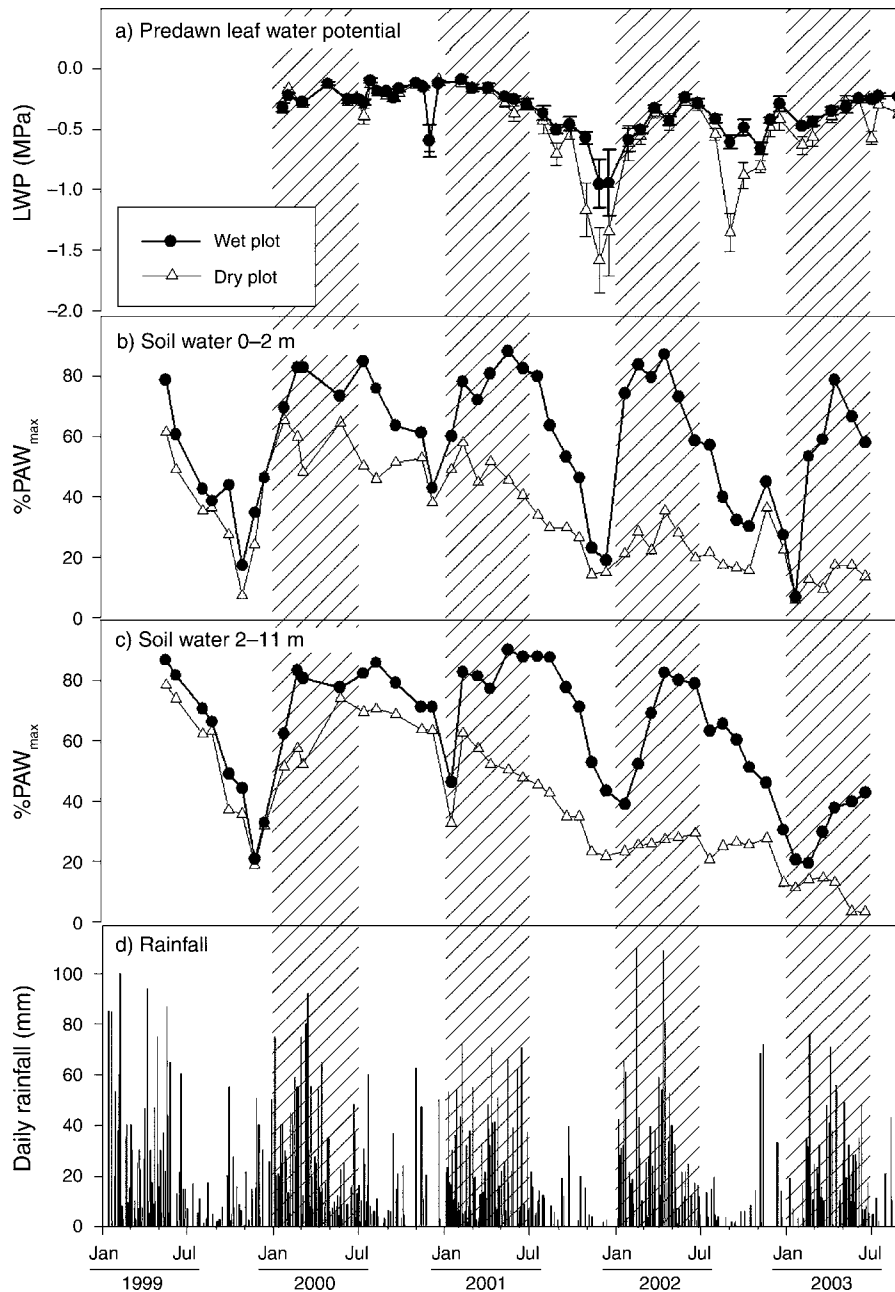


FIG. 2. Selected components of the water balance within the wet (W) and dry (D) plots at the Tapajós throughfall exclusion experiment, showing (a) predawn leaf water potentials averaged across six species (mean  $\pm$  SE;  $n = 3$  trees per species,  $n = 4$  leaves per tree) in both plots; (b) plant-available soil water as a percentage of the maximum value (%PAW<sub>max</sub>) for 0–2 m; (c) %PAW<sub>max</sub> for 2–11 m in the soil profile; and (d) daily precipitation. Vertical hatching indicates periods when the throughfall exclusion system was functioning during the wet season.

conducted (Fig. 3a). There were 242 tree, liana, and palm species common to both plots, representing 73% and 63% of the total number of species encountered in the D ( $n = 339$ ) and W ( $n = 392$ ) plots, respectively. The distribution of species across life forms was nearly identical in both plots: trees represented  $\sim 78\%$ , lianas 21%, and palms the remaining 1% of the total number of species in the study plots. Considering only life forms,

trees composed 88% (W) and 86% (D), lianas 11% (W), and 13% (D), and palms 1% (W) and 2% (D) of stems  $> 2$  cm dbh. The distribution of trees by potential canopy positions was likewise similar in both plots. Small-diameter trees (2–5 cm dbh) were the most abundant size class for each of the three canopy position categories in both plots. About 50% of all potential overstory and midcanopy species were represented as

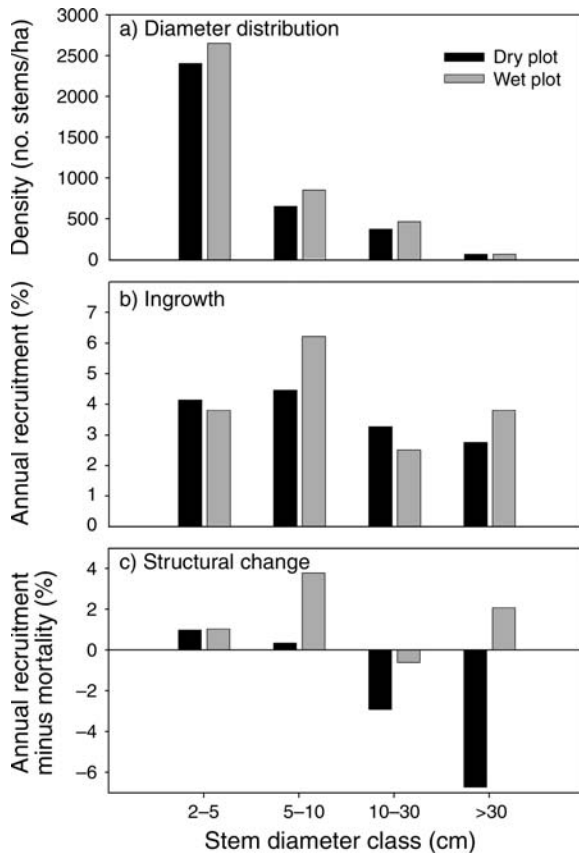


FIG. 3. Aspects of forest structure at the study site, showing (a) the distribution of stems by diameter size class in the wet (W) and dry (D) plots at the time of the first inventory in March 2000; (b) stem recruitment rates by size class over the interval between the initial inventory and August 2003 (ingrowth refers to stems that advanced to a larger diameter class through stem growth). Part (c) shows the percentage change in numbers of stems in each size class based on the difference between mortality and recruitment rates.

juvenile saplings and 87% of all understory species were represented as small trees falling into this size class.

Reduced growth rates (D. Nepstad, D. Ray, and P. Brando, *unpublished data*) and increased mortality changed recruitment patterns in the D plot. Despite average recruitment rates of  $\sim 3$ – $6\%$ /yr across all size classes in both plots, mortality in the larger size classes surpassed recruitment in the dry plot (Fig. 3b, c). Drought-induced mortality exceeded recruitment by  $2.9\%$ /yr and  $6.7\%$ /yr for stems 10–30 cm dbh and  $>30$  cm dbh, respectively (Fig. 3c). By contrast, mortality was offset by recruitment among smaller diameter plants, thereby maintaining a positive structural change in the 2–5 cm and 5–10 cm size classes. Thus, the net effect of the drought treatment on forest structure was a 10% reduction in the number of larger trees ( $\geq 10$  cm dbh).

Partial throughfall exclusion amplified mortality rates among all stems, but particularly for the larger trees

(Fig. 4a). Following 3.2 yr of measurements, the community-wide mortality rate in the D plot ( $3.77\%$ /yr) significantly exceeded the W plot mortality rate ( $2.72\%$ /yr) by 38% ( $P < 0.001$ ). Only the smallest size class, 2–5 cm, did not undergo significantly greater mortality rates in the D plot ( $P = 0.13$ ). In all other size classes mortality rates were considerably greater in the dry plot than in the wet plot. Mortality rates were 69% higher in the dry plot than the wet plot in the 5–10 cm size class, 98% greater in the 10–30 cm size class, and 445% higher in the  $>30$  cm size class (Fig. 4a). Independent of stem size, lianas demonstrated a greater susceptibility to drought than either trees or palms (Fig. 4b). The mortality rate for lianas was  $\sim 70\%$  greater in the dry plot,  $6.78\%$ /yr, than in the wet plot,  $3.78\%$ /yr ( $P = 0.004$ ). Trees endured significantly higher mortality in the D plot,  $3.36\%$ /yr, than in the W plot,  $2.54\%$ /yr, ( $P = 0.009$ ). Palms also underwent higher mortality rates of similar magnitude to that of trees; however, the sample

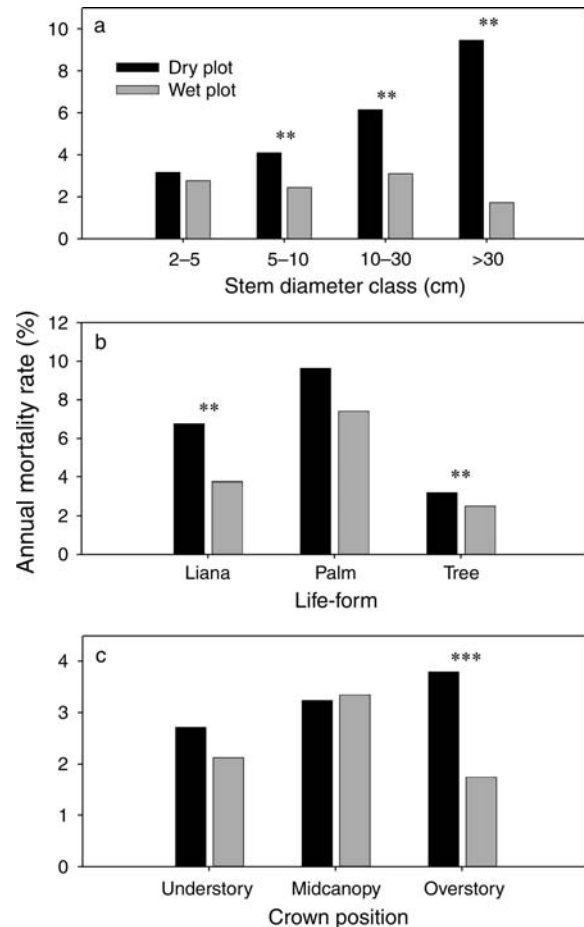


FIG. 4. Annual mortality rates for different groupings of vegetation in the wet (W) and dry (D) plots. Groupings include (a) four diameter size classes, (b) three life forms, and (c) three tree canopy positions. Asterisks above the paired bars indicate a significantly higher mortality rate in the D than in the W plot (one-tailed Fisher's exact test: \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

size was much smaller for palms and the difference was not significant ( $P = 0.402$ ).

Tree species that potentially grow to reach the upper canopy at maturity were more vulnerable to drought than those potentially reaching only the midcanopy or understory (Fig. 4c). Mortality rates were more than double in D than in W for the overstory species ( $m_W = 1.75\%/yr$ ,  $m_D = 3.80\%/yr$ ;  $P < 0.0001$ ), but remained similar for the midcanopy species ( $m_W = 3.35\%/yr$ ,  $m_D = 3.24\%/yr$ ;  $P = 0.44$ ), and only modestly elevated among the understory species ( $m_W = 2.52\%/yr$ ,  $m_D = 3.18\%/yr$ ;  $P = 0.087$ ). Mortality rates and 95% confidence intervals for all species in both plots are listed in the Appendix.

#### *Medium- and large-tree survivorship*

Changes in soil water and associated drought stress resulting from the treatment are the best indicators of large-tree mortality responses to drought. Elevations in large-tree mortality were delayed until late in the third dry season of the water exclusion treatment, when %PAW<sub>max</sub> reached its lowest levels in both 0–2 and 2–11 m depth intervals (Figs. 2 and 5). When the large-tree mortality response was triggered, trees exceeding 30 cm dbh underwent the fastest decline in survivorship. From the middle of the third to the fourth dry season of the study period, the 10–30 cm size class declined from 94% to 84% of its initial population in the D plot and from 95% to 93% in the W plot (Fig. 5a). In the same sampling interval the >30 cm size class declined by 21% of its initial population, from 100% to 79%, in the D plot and remained at 95% survivorship in the W plot (Fig. 5b).

The difference between the two plots in survivorship of medium and large trees appears to be associated with a threshold difference in the plots' water stress integral. Prior to an accumulation of 100 MPa-days (the unit of the WSI; see *Methods: Plant-available water and leaf water potential*) of differential water stress between the two plots in October 2002, there was no relationship between water stress integral (WSI) and large-tree survivorship (Fig. 5c). However in November 2002, the plots crossed a difference threshold of 100 MPa-days WSI and a positive association between WSI and large-tree survivorship emerged. Subsequently, as the WSI increased from 100 to 120 MPa-days, survivorship of the original population of large trees in the W plot exceeded the D plot by >10%. The escalating WSI in the D plot during the fourth throughfall exclusion period in 2003 indicates that wet season recharge was insufficient to curb drought stress.

The delayed mortality response in medium and large trees was also linked to the cumulative changes in PAW throughout the soil profile. Prior to the declines in large-tree survivorship in the D plot, PAW fell below 30% PAW<sub>max</sub> for the entire soil profile (0–11 m) in October 2001 (Fig. 2). Subsequently, soil water was maintained below 30% PAW<sub>max</sub> in the D plot for the rest of the study period, except for a brief spike in November 2002

at 0–2 m depth due to heavy rains during the dry season. In contrast, %PAW<sub>max</sub> in the W plot dropped below 30% only at the end of the 2002 dry season. Unlike the protracted reduction in the D plot, this brief decline in %PAW<sub>max</sub> in the W plot was not accompanied by increased tree mortality. The cumulative difference in PAW between the two plots rose gradually for the 0–2 m profile for the duration of the study period, but increased markedly for the 2–11 m profile, particularly after the 2001 dry season (Fig. 5d).

#### *Biomass and dead biomass (necromass)*

The aboveground standing biomass of stems  $\geq 2$  cm dbh was slightly higher in the D plot (310.6 Mg/ha) than in the W plots (302.6 Mg/ha) in March 2000, when the initial inventory was completed (Fig. 6a). At that time stems >10 cm dbh accounted for ~90% of the pretreatment standing live biomass in both plots. Drought-induced mortality generated a large net increase in the amount of dead biomass in the D plot. Following four seasons of the treatment, the total quantity of aboveground dead biomass was 46.5 Mg/ha greater in the D plot (65.9 Mg/ha) than in the W plot (19.4 Mg/ha). Furthermore, unlike the W plot, the change in standing biomass in the D plot failed to offset the dead biomass pools created (Fig. 6b). These changes represent a net increase of "committed emissions to the atmosphere" of  $7.3 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  over the study period (Fig. 7). Transfer of live biomass to the dead biomass pool represents "committed" carbon emission, insofar as most of it will eventually be released to the atmosphere through decay (Fearnside 1997). Larger diameter stems (>10 cm dbh) accounted for 95% of the total dead biomass generated, reflecting both their relatively higher mortality rates and C content. Inputs to the dead biomass pool were approximately two times higher for the 5–10 and 10–30 cm dbh size classes and over five times greater for the >30 cm dbh size class in the D plot than in the W plot.

#### DISCUSSION

The seasonally dry forest of the Tapajós is an extremely drought-tolerant ecosystem. Our partial throughfall exclusion simulated effective rainfall of 1120, 1130, and 630 mm during the second through fourth years of the study period (eight months in the final year), well below evapotranspirational water loss of ~1400–1500 mm/yr measured at this site during the same period (Saleska et al. 2003). But, surprisingly, the mortality of large trees (>10 cm dbh) began only during the final year of the experiment (Fig. 5). This drought tolerance is conferred in part by deeply penetrating root systems that absorb soil water to depths of at least 11 m (Nepstad et al. 1994, 2004, Moreira et al. 1997, Jipp et al. 1998, Bruno et al. 2006). It may also be facilitated by hydraulic redistribution of soil water documented at this site (Oliveira et al. 2005), in which the nighttime flow of soil water upward through vertical roots and then away

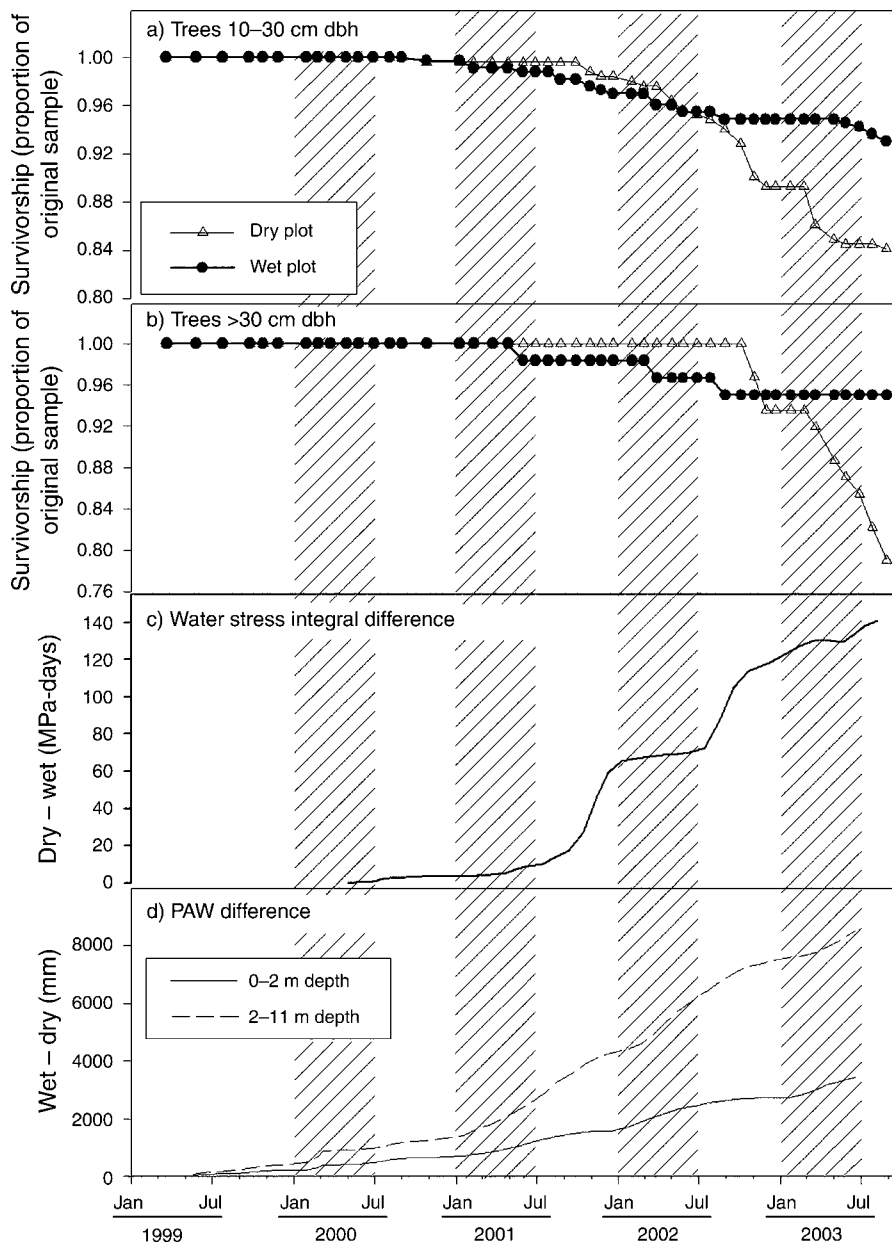


FIG. 5. Survivorship curves for trees (a) 10–30 cm dbh and (b) >30 cm dbh sampled monthly in the wet (W) and dry (D) plots at the throughfall exclusion experiment; (c) relative differences between plots in terms of the cumulative water stress integral; and (d) cumulative differences in plant-available soil water for two depth intervals in the soil profile. Vertical hatching indicates periods when the throughfall exclusion system was functioning during the wet season.

from the stem into the soil via lateral roots facilitates subsequent daytime water uptake from shallow soils. Finally, drought tolerance may be associated with significant uptake of water directly by leaves during dry season rains and nighttime dew events, also documented at this site (G. Cardinot, M. Moreira, L. Sternberg, D. Nepstad, R. Oliveira, T. Dawson, and S. Burgess, *unpublished manuscript*).

The study supports the hypothesis that the mortality of large trees increases precipitously when soil water

reaches a critical minimum threshold. Mortality of medium-sized trees (10–30 cm dbh) and large trees (>30 cm dbh) increased dramatically as the water stress integral difference reached 100 MPa-days (Fig. 5). The very high levels of mortality during ENSO drought observed in Borneo and Sumatra (Leighton and Wirawan 1986, Kinnaird and O'Brien 1998, Nakagawa et al. 2000, Aiba and Kitayama 2002, van Nieuwstadt and Sheil 2005) may have been associated with the depletion of soil water below a critical minimum



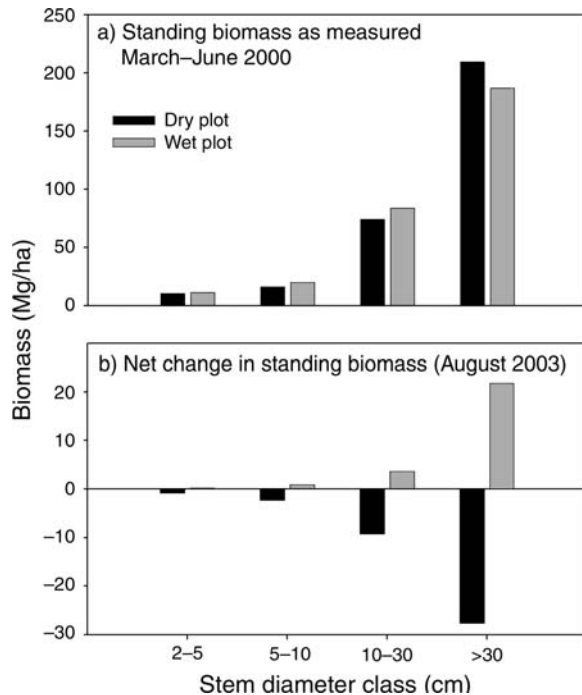


FIG. 6. (a) Standing biomass distribution by size class at the time of original inventory in June 2000. (b) Net change in biomass for each size class by the time of the August 2003 inventory.

threshold—a threshold that varies with rooting depths, plant physiological tolerance to drought, impenetrable horizons, soil texture, and rainfall. Relatively mild soil water depletion may provoke greater tree mortality in these aseasonal forests if they are composed of trees that are physiologically drought sensitive or unable to obtain water during extended periods of drought through deep rooting or other mechanisms.

Both the synchrony of the tree mortality response for the two tree size classes and the relatively low rates of small-stem mortality observed for the size classes <10 cm dbh (Fig. 4) argue against the hypothesis that there is an initial drought response in which the mortality of small trees is greatest because of their shallower rooting depths (Fig. 4). However, the study results support the hypothesis that lianas, like large trees, are susceptible to drought-induced mortality. In addition to their exposure to solar radiation, this drought response may be associated with their vulnerability to xylem cavitation (Schnitzer and Bongers 2002). This response is also consistent with observations of deep root systems (Restom and Nepstad 2004); lianas may avoid drought-induced mortality or tissue damage by tapping deep soil moisture, but are vulnerable to mortality when deep soil moisture is depleted. The trend toward increasing densities of lianas in recent years, indicated by permanent plot studies (Phillips et al. 2005), could be dampened under scenarios of increasingly severe drought episodes.

The degree to which the Tapajós is representative of other tropical forests subjected to episodic severe drought must be evaluated using both climatic and edaphic criteria. The rainfall regime of this forest is similar to approximately one-third of the Amazon forest formation in both total annual amount and seasonal distribution (Nepstad et al. 2004).  $PAW_{max}$  to 10 m depth (1100 mm) is lower than all but 10% of the Basin (Nepstad et al. 2004). The total annual rainfall that we simulated during the second and third years of the experiment (1120 and 1130 mm/yr) (Fig. 1) is lower than all but 5% of the forests of the Amazon for any given year during the period 1996–2004 (Nepstad et al. 2004, updated with recent rainfall data), but is within the range of values already measured at the Tapajós site. The effective rainfall induced by this experiment is rare in the Amazon today, but could become much more common in the future through climate change (Oyama and Nobre 2003, Cox et al. 2004).

Soil water content can be strongly influenced by groundwater, which is deeper in the Tapajós forest (100 m) than in much of the Amazon (Costa et al. 2002). Shallow water tables that can be reached by tree root systems may increase soil water availability. (In the long term, however, transpirational uptake of groundwater will lower its level, unless the aquifer is being recharged elsewhere.) The water table is dynamic in regions of seasonal rainfall, varying by up to 8 m in some forests (Nepstad et al. 1994), recharging the moisture of soils dried through transpirational uptake. Little is known, however, of the ability of root systems to survive the low oxygen levels that develop when the water table rises, and it is possible that forests on soils with shallow water tables experience annual dieback of deep root systems as they become submersed. Further research is needed to determine the influence of depth to water table on the drought tolerance of moist tropical forests.

The simulated drought transferred nearly 30 Mg/ha of live aboveground biomass to the dead biomass pool

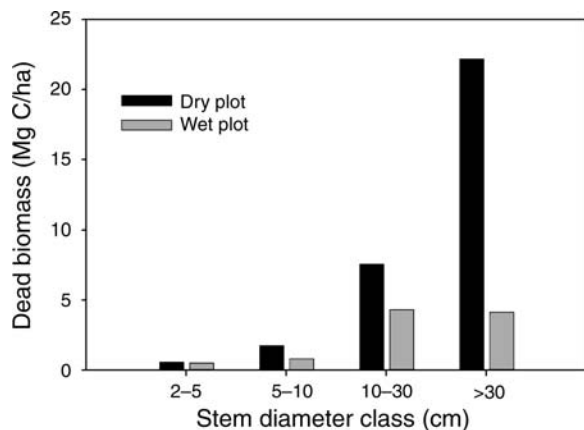


FIG. 7. Quantity of dead biomass, presented as “committed carbon,” in both plots for each size class by the August 2003 inventory (see *Results: Biomass and dead biomass*).

through the death of medium and large trees and may have reduced growth of the live biomass pool by another 20 Mg/ha (Figs. 6 and 7). The effect of the increase in dead biomass on forest carbon exchange with the atmosphere will be determined by the balance between dead biomass decomposition rates, the rate of further additions to this dead biomass pool from posttreatment mortality, and the posttreatment accumulation of photosynthetically fixed carbon in new wood (5 Mg/ha in the control plot). The long-term effect of a severe drought such as the one simulated would depend upon other ecological and economic processes underway in the landscape. For example, the posttreatment forest has lower leaf area index and higher light penetration than the undisturbed forest, with abundant fuels from collapsing trees and new light-dependent colonizing trees and grasses. Where propagules of grasses and forbs are available from neighboring cattle pastures and crop fields, drought-induced tree mortality can open moist tropical forests to invasion from these highly flammable, light-demanding plants, increasing the likelihood that the forest will catch fire, and initiating a positive feedback of further tree mortality and increasing flammability (Nepstad et al. 2001).

Coupled climate and vegetation models designed to simulate future interactions between terrestrial ecosystems and climate currently capture some of these processes through the gradual displacement of one plant form by another as climatic changes shift competitive advantages (e.g., Oyama and Nobre 2003, Cox et al. 2004). Episodic events, such as severe droughts, may accelerate these simulated vegetation shifts through mortality of centuries-old canopy trees. Current emissions of carbon to the atmosphere from tropical deforestation comprise approximately one-fifth of global average anthropogenic emissions (Prentice et al. 2001), and these emissions could increase through the combined effect of severe episodic drought and fire.

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#### APPENDIX

Annual percentage mortality rates and 95% confidence intervals for paired and unpaired species in wet and dry plots, in the Tapajós National Forest, east-central Brazilian Amazon (*Ecological Archives* E088-136-A1).