Amazonian Tree Mortality during the 1997 El Niño Drought

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Abstract: *In 1997, the Amazon Basin experienced an exceptionally severe El Niño drought. We assessed effects of this rare event on mortality rates of trees in intact rain forest based on data from permanent plots. Long-term (5- to 13-year) mortality rates averaged only 1.12% per year prior to the drought. During the drought year, annual mortality jumped to 1.91% but abruptly fell back to 1.23% in the year following El Niño. Trees dying during the drought did not differ significantly in size or species composition from those that died previously, and there was no detectable effect of soil texture on mortality rates. These results suggest that intact Amazonian rainforests are relatively resistant to severe El Niño events.*

Mortandad de Arboles del Amazonas Durante la Sequía de El Niño de 1997

Resumen: *En 1997 la Cuenca Amazónica sufrió una de las sequías más severas de este siglo, asociada al fenómeno meteorológico El Niño. Usando parcelas permanentes determinamos la mortandad de árboles antes, durante, y después de El Niño de 1997. La tasa de mortandad de largo plazo (5-13 años) promedió tan solo un 1.12% anual antes de la sequía. Durante el año de la sequía, la mortandad anual aumentó a un 1.91%, pero disminuyó abruptamente a un 1.23% al año siguiente de El Niño. No se encontraron diferencias significativas en el tamaño ni en la composición de especies entre los árboles que murieron durante la sequía comparados con los árboles que habían muerto previamente. Tampoco se detectó un efecto de la textura del suelo sobre la tasa de mortandad. Concluimos que los bosques primarios de la Cuenca Amazónica son relativamente resistentes a los efectos asociados a eventos severos de El Niño.*

Introduction

In 1997–1998, the Amazon Basin experienced a severe drought, associated with what many consider the strongest El Niño–Southern Oscillation (ENSO) event of this century (Marengo & Tomasella 1998; Hammond & Steege 1998; McPhaden 1999). Severe effects of this El Niño have been documented in the eastern Amazon, where previously logged, secondary forests suffered incursions by fire (Cochrane et al. 1999). In contrast, large tracts of primary forests of the central Amazon were not penetrated by fire but nevertheless, experienced extreme drought. We present the first record of the magnitude of the drought-induced mortality for these rainforest trees.

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Methods

The study area is located in the central Amazon (lat2°20'S, long 59°50'W) about 80 km north of Manaus, Brazil, and includes 12 permanent 1-ha plots in the interior (>230 m from the nearest clearing) of a large tract of primary rainforest (>10^6 ha) that is part of the Biological Dynamics of Forest Fragments Project (BDFFP; Lovejoy & Bierregaard 1990). The plots are in two BDFFP reserves (1301 and 1501) separated by 12 km and located in continuous old-growth forest. With rainfall averaging over 2000 mm per year, the study area is within the "Am" classification of Köppen (1936), indicating a tropical, humid climate with several months of excessive rainfall and 1–2 months of seasonal drought.

We compared mortality rates of large (≥10 cm in diameter at breast height [dbh]) trees at the sites before, during, and after the 1997 ENSO drought. We estimated mortality rates before the drought based on surveys of each plot over one to three intervals each of 3–5 years, the total time varying from 5.2 to 13.7 years per plot. For some plots, these intervals included locally weak ENSO events in 1986–1987 and 1992–1993, neither of which produced a detectable effect on tree mortality in the reserves. We determined mortality rates for 12–16 months during the 1997 drought and for 12–13 months after the drought with identical surveys (Table 1). At each survey, we considered a tree to be dead if it lacked foliage and sap in the secondary vascular tissue. We measured tree diameters at 1.3 m height except for buttressed trees, which we measured above the buttresses to avoid overestimating diameters (Clark & Clark 1996). All trees were identified to species or morphotype.

For each survey, we calculated annualized rates of tree mortality as $r = 1 - (N_t/N_0)^{1/t}$, where N_0 is the number of trees at the beginning of the interval, t is the time interval, and N_t is the number of trees of the original N_0 that are alive at the end of the interval (Sheil & May 1996). Because there was no significant relationship between mortality rate and survey interval, no correction of the rates based on interval length was necessary ($p = 0.84$, $t = 0.21$, df = 7, paired t test, for eight plots with both short [11- to 45-month] and long [102- to 119-month] intervals).

For reserve 1501, we compared daily rainfall during the 1997 drought to rainfall of the previous 7 years (1990–1996), measured with a cylindrical rain gauge. Because we expected that clay content might influence soil water-holding capacity and, consequently, tree mortality during the drought, we also determined clay content (particles <0.002 mm diameter) of soils for eight of the plots based on 220–260 soil surface samples (<20 cm depth) per plot.

Results

Only 230 mm of rain fell during the 1997 dry season (June–October), whereas the average for the previous 7 years was 732 mm. Thirty-day moving averages revealed 146 consecutive days (26 June–18 November 1997) below 100 mm rainfall and 62 consecutive days (11 September–11 November) below 40 mm (Fig. 1). The intensity of the drought increased as the dry season progressed, until it was ended abruptly by heavy rains in mid-November (Fig. 1). This pattern clearly differed from the pre-drought period, during which the 30-day moving average never fell below 100 mm and the seasonal drought intensified only into September before reversing course.

In 1997 there were 623 ± 23 (mean ± SD) trees per plot. Pre-ENSO mortality averaged 1.12% per year or about 7 trees/ha (Table 1). During the drought, tree mortality increased in 11 of the 12 plots, rising significantly to a mean of 1.91% ($p = 0.004$, paired t test = 3.56; Table 1). In the post-ENSO year, mortality declined

Table 1. Survey details and annualized rates of tree mortality (10-cm diameter at breast height) in the central Amazon before, during, and after the severe 1997 El Niño–Southern Oscillation (ENSO) drought.

	Reserve		*Both reserves*
	1501	*1301*	
Survey intervals			
pre-ENSO	1991–1996	1983/87–1996	
1997-ENSO	12/96–7/98	4/97–6/98	
post-ENSO	7/98–8/99	6/98–7/99	
Sample sizes			
1-ha plots	3	9	12
trees	1951	5525	7476
Annualized mortality rates (%/year, $\bar{x}$ ± SD)			
pre-ENSO	0.94 ± 0.28	1.19 ± 0.67	1.12 ± 0.59
1997-ENSO	1.88 ± 0.56	1.92 ± 0.69	1.91 ± 0.64
post-ENSO	1.64 ± 0.87	1.10 ± 0.42	1.23 ± 0.57

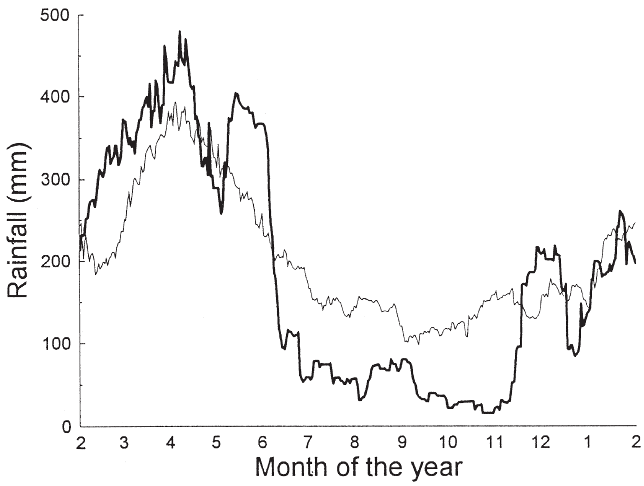

Figure 1. Thirty-day moving averages for rainfall during the 1997 El Niño–Southern Oscillation (ENSO) drought (heavy line) and during pre-ENSO years (fine line). Months run from February (2) of one year to February of the next year.

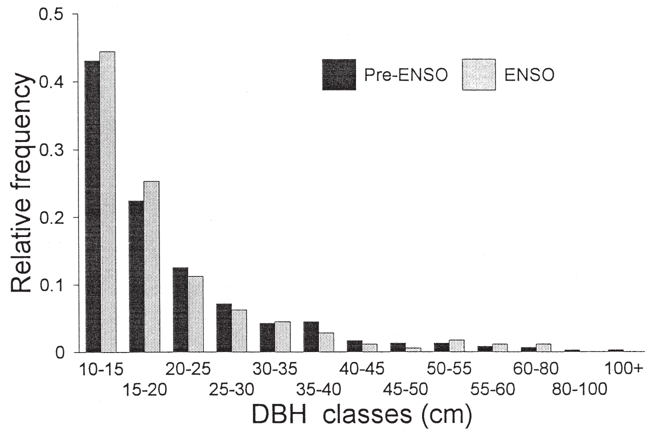

Figure 2. Frequency distributions of diameter at breast height (dbh) of dying trees during the 1997 El Niño Southern-Oscillation drought and during the pre-drought years.

in all 12 plots to a mean of 1.23%, which was significantly lower than the ENSO mortality ($p = 0.001$, $t = 4.58$) and not different from the pre-ENSO mortality ($p = 0.68$, $t = 0.43$).

Standard deviations of mortality rates across the 12 plots remained nearly constant across pre-ENSO, ENSO, and post-ENSO intervals (Table 1). Mortality rates were not significantly different between the two reserves (pre-ENSO, $p = 0.55$, $F_{1,10} = 0.38$; ENSO, $p = 0.93$, $F_{1,10} = 0.01$; post-ENSO, $p = 0.17$, $F_{1,10} = 2.24$, one-way analysis of variance; Table 1). Mortality rates were not correlated significantly between the pre-drought and drought intervals ($r = -0.17$, $p = 0.60$) or between the pre-drought and post-drought intervals ($r = -0.13$, $p = 0.68$). There was, however, a significant, positive correlation between the drought and post-drought intervals ($r = 0.65$, $p = 0.02$; Pearson correlations).

There was no difference in the size distributions of trees dying during ($n = 178$) and before ($n = 776$) the drought ($D = 0.04$, $p = 1.00$, Kolmogorov-Smirnov test; Fig. 2). Mortality during the drought was roughly proportional to species abundances, with the 178 tree deaths spread over 131 species. Most species had no deaths (521 species) or one death (106 species). Only 25 species had more than 1 death, and only 1 had more than 5 deaths. That species, *Oenocarpus bacaba* Mart., is an abundant subcanopy palm that lost 10 trees and had the only mortality rate (7.0%) significantly above the mean ENSO rate ($p = 0.006$, proportion test). Mortality rates significantly below the mean were undetectable with these sample sizes.

Clay content varied from 30% to 66% across the eight plots sampled and was not correlated with mortality rates for any interval (pre-drought, $r = -0.21$, $p = 0.60$; drought, $r = 0.05$, $p = 0.90$; post-drought, $r = 0.20$, $p = 0.63$; Pearson correlations).

Discussion

For many Amazonian trees, the overt symptoms of water stress, such as leaf wilt and abscission, were evident during the 1997 drought. Tropical rainforests typically suffer drought when precipitation falls below 100 mm per month, and severe stress at <50 mm per month (Whitmore 1984; Richards 1996), so the recorded 30-day averages of 146 consecutive days below 100 mm and 62 days below 40 mm appear severe and unusual for the central Amazon (Fig. 1).

The drought-year mortality increase from 1.12% to 1.91% in our study area is modest in comparison with the findings of the few other studies of ENSO effects on tropical forests. Mortality rates in unburned rainforests in Indonesia were an order of magnitude higher during the ENSO droughts of 1997–1998 (approximately 10%; Kinnaird & O'Brien 1998) and 1982–1983 (14–24%; Leighton & Wirawan 1986). Pre-drought rates were not available for these studies, but baseline mortality is 1–3% per year in comparable Asian rainforests (Phillips et al. 1994). In Panama during the 1982–1983 ENSO, annual tree mortality (≥10 cm dbh) averaged 2.75% from 1982 to 1985 compared with 1.98% for the post-drought interval of 1985–1990 (Condit et al. 1995). The magnitude of the mortality increase (0.77%) in Panama was similar to what we found in the central Amazon (0.79%), but the increase in Panama was probably diluted by including both drought and nondrought years in the 1982–1985 interval. If the nondrought years had typical mortality

(1.98%), then the drought year would have had about 4.29% mortality to produce a mean of 2.75% from 1982–1985. Although 4.29% mortality is much lower than that observed in Indonesia, it is more than double the rate we observed for the central Amazon.

Alternatively, one might view our drought-related rise in annual mortality (from 1.12% to 1.91%) as substantial because it represents a relative increase of 71%. Such an increase would have a significant effect on the forest if it were maintained for many years. In the year after the drought, however, mortality dropped back to 1.24%, a rate not significantly different from that before the drought. Thus, in the intact forests of our study area, the effects of the unusually severe 1997 ENSO were apparently short-term in nature. Severe El Niño droughts have occurred at most four times in the Amazon this century (Marengo & Tomasella 1998); so they are not common events.

Other attributes of the 1997 drought suggest that there was little pervasive change in the forest. First, mortality rates in 1997 were not significantly correlated with those during the pre-drought interval. The absence of such correlations between successive inventories has been a general feature of the BDFFP network of permanent plots during non-ENSO intervals, and it remained so in 1997 despite an overall increase in mortality. Second, there was little evidence of strong size- or species-specific mortality during the drought. In contrast, during the 1982–1983 drought, tropical trees in Panama and Borneo both exhibited striking differences in mortality based on tree size and growth habit, with larger canopy trees being most vulnerable (Leighton & Wirawan 1986; Condit et al. 1995). Finally, mortality during the drought was unrelated to soil clay content in our study area. In Borneo, mortality of large trees during the 1982–1983 ENSO was much higher on well-drained ridges and slopes than on adjacent alluvial soils (Leighton & Wirawan 1986), although similar results were not observed in Panama (Condit et al. 1995).

In summary, the only evidence for lingering effects of the 1997 drought in the central Amazon were the excessive loss of one palm species and the fact that mortality rates during and after the drought were significantly correlated, perhaps implying a residual, time-lag effect on tree survivorship. Therefore, we conclude that the 1997 drought had only a modest effect on tree mortality in our study area. Given the exceptional severity of the 1997 ENSO, it appears that continuous, old-growth forests of the central Amazon basin are relatively resistant to drought. Drought resistance in rainforest trees is known to be a function of stand age (Kaufman & Uhl 1990) and distance from forest edges (Laurance et al. 1997, 1998). Old-growth forests retain moisture more effectively than do fragmented or secondary forests. Thus, conservation of intact central Amazonian forests seems feasible even in the face of extreme climatic variation, at least where large tracts of unlogged rain forests remain.

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