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Biomass change in an Atlantic tropical moist forest: the ENSO effect in permanent sample plots over a 22-year period

Received: 13 February 2004 / Accepted: 31 August 2004 / Published online: 29 September 2004
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Abstract There are a number of controversies surrounding both biomass estimation and carbon balance in tropical forests. Here we use long-term (from 1978 through 2000) data from five 0.5-ha permanent sample plots (PSPs) within a large tract of relatively undisturbed Atlantic moist forest in southeastern Brazil to quantify the biomass increment (ΔM_I), and change in total stand biomass (ΔM_{stand}), from mortality, recruitment, and growth data for trees ≥ 10 cm diameter at breast height (DBH). Despite receiving an average of only 1,200 mm annual precipitation, total forests biomass ($334.5 \pm 11.3 \text{ Mg ha}^{-1}$) was comparable to moist tropical forests with much greater precipitation. Over this relatively long-term study, forest biomass experienced rapid declines associated with El Niño events, followed by gradual biomass accumulation. Over short time intervals that overlook extreme events, these dynamics can be misinterpreted as net biomass accumulation. However for the 22 years of this study, there was a small reduction in forest biomass, averaging $-1.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (± 3.1). Strong climatic disturbances can severely reduce forest biomass, and if the frequency and intensity of these events increases beyond historical averages, these changing disturbance regimes have the capacity to significantly reduce forest biomass, resulting in a net source of carbon to the atmosphere.

Keywords Disturbance · Climate change · ENSO · Drought · Tree mortality

Introduction

Tropical permanent sample plots (PSPs) have been utilized to predict the impacts of environmental change on vegetation-related processes. Some results from PSPs indicate that mature neotropical forests are a net sink for atmospheric carbon due to increasing forest biomass (Phillips et al. 1998, 2002a, b; Baker et al. 2004; Lewis et al. 2004). Measurements over shorter time scales using the eddy covariance method in tropical forests also suggested a net carbon sink (Grace et al. 1995; Malhi et al. 1998), but other PSP studies (Clark 2002; Chave et al. 2003), and recent studies using eddy covariance in conjunction with detailed field data (Saleska et al. 2003; Chambers et al. 2004b) suggest that at least some neotropical forests are probably best characterized as in a state of dynamic equilibrium.

Tropical forests contain about 40% of the carbon stored as terrestrial biomass (Dixon et al. 1994) and represent a substantial fraction of the world's forest NPP (Melillo et al. 1993; Field et al. 1998). Field estimates of net primary production (NPP) for tropical ecosystems are important to assess carbon cycling rates in the face of global changes, and to validate global-scale ecosystem models (IPCC 2001). Field studies for estimating forest NPP involves measurements of separated below- and above-ground components, which include the increments and losses of forest biomass throughout the time period (Clark et al. 2001b). Above-ground biomass increment or stand mass increment (ΔM_I , Chambers et al. 2001; Clark et al. 2001a, b), is an important component of NPP, and is defined as the change in mass of surviving trees in an inventory plot over time. In a recent detailed review of available data for estimating total NPP from 39 old-growth tropical forest sites, Clark et al. (2001a) found that only 18 of the

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these sites had reliable information to accurately quantify ΔM_1 , which varied from 0.3 to 3.8 Mg C ha⁻¹ per year.

Another important variable for calculating forest carbon balance is the total change in tree stand mass over time (ΔM_{stand}), which is the sum of recruitment and ΔM_1 , less mortality. Since tree mortality in tropical forest is highly episodic in space and time, ΔM_{stand} is generally much more variable than ΔM_1 . In addition, recent studies find that elevated tree mortality in particular years is strongly linked to changes in environmental conditions. For example, a dramatic decline in precipitation correlated with a strong El Niño event resulted in much higher than average tree mortality rates at sites distributed throughout the neo-tropics (Condit et al. 1995, 1996; Laurance et al. 2001; Rolim et al. 1999, 2001).

Here we use long-term (from 1978 through 2000) data from five 0.5-ha PSPs within a large tract of relatively undisturbed Atlantic moist forest in southeastern of Brazil to quantify ΔM_1 and ΔM_{stand} from mortality, recruitment, and growth data for trees ≥ 10 cm diameter

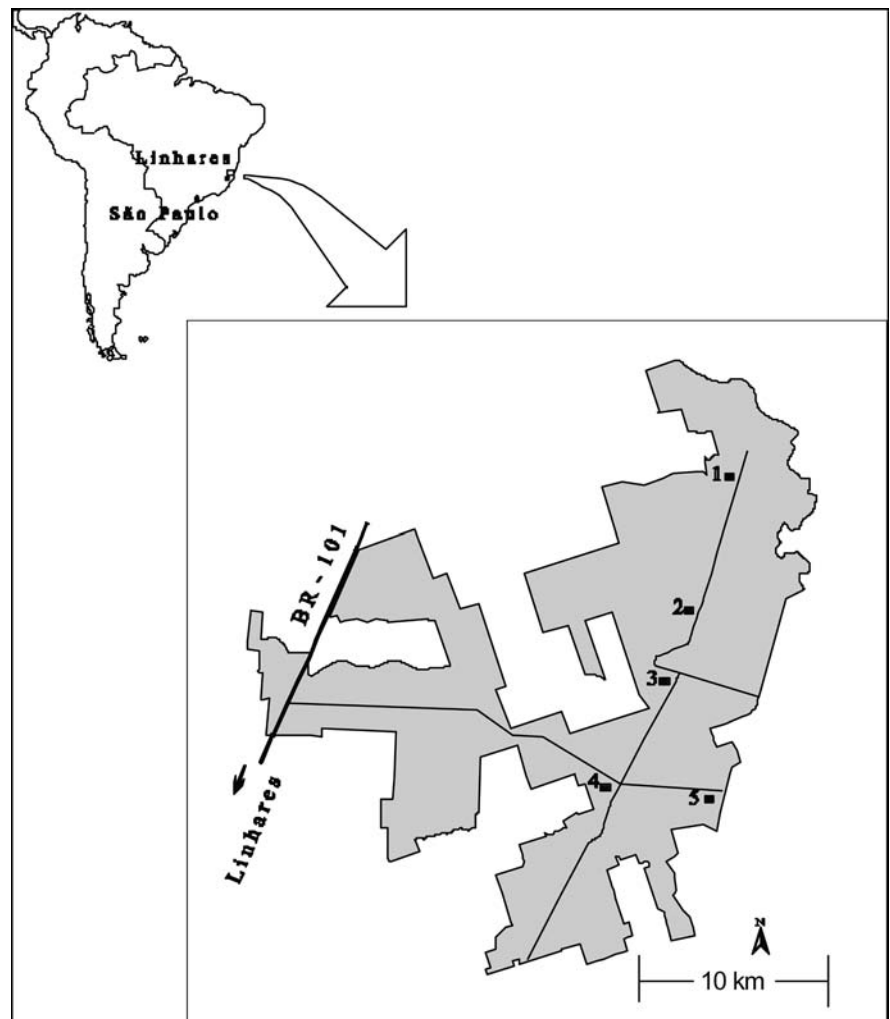
at breast height (DBH). To provide substantive information on biomass dynamics from year to year, each plot was recensused ten times at 1–5.5 year intervals during the 22-year period (since 1983). Long-term PSP data with numerous census over short time intervals is quite rare for tropical forests (Clark et al. 1993), and PSP data for Atlantic forest is particularly lacking. We addressed specific hypotheses related to how both short-term and long-term biomass dynamics parameters are affected by differences in annual tree mortality, growth, and recruitment as a consequence of extreme changes in rainfall in particular years.

Materials and methods

Study site

This study was conducted at Vale do Rio Doce Reserve (RVRD), which is located about 30 km north of the city of Linhares, Espírito Santo state, Brazil (19°18' S and

Fig. 1 Location and map of Linhares Natural Reserve, Brazil. The plots in the map indicate the blocks of experimental study



40°04' W), with an elevation of 28–65 m (Fig. 1). The reserve is 21,787 ha in size and one of largest tracts of intact Atlantic rain forest in Brazil. The adjoining matrix is a mix of pasture, cultivated lands (papaya, coffee), and timber plantations (*Eucalyptus*). The reserve was created in the 1950s when the Brazilian company Companhia Vale do Rio Doce (CVRD) planned to use timber from the site to fabricate railroad ties for the Vitória-Minas line. Forest management studies indicated that the plan was not economically viable, and the forest site was maintained as a reserve. Numerous long-term studies are being carried out in RVRD in primary and secondary forests, in plantations with arboreal species, and on seed ecology.

The forest is semi-deciduous with about 30% of the species ($n=41$) losing their leaves in the dry season (Engel 2000). The five study plots are located on a large plain with little topographic variability. The soil that occurs on the PSPs is a nutrient-poor dystrophic red-yellow podzol (Peixoto and Gentry 1990, site 13 in Clinebell et al. 1995), which is the dominant soil type in the Linhares reserve (Garay et al. 1995).

Systematic surveys have been undertaken in the Reserve during the past 25 years and the CVRD herbarium at the reserve contains a collection of 10,000 specimens, representing more than 2,100 vascular plant species. Forest composition is similar to that of most neo-tropical humid lowland forests, with accentuated species richness in the families Leguminosae, Myrtaceae, Annonaceae, Sapotaceae, Rubiaceae and Bignoniaceae (Peixoto and Silva 1997; Peixoto et al. 2004; Rolim and Chiarello 2004). Myrtaceae is the most species-rich family if Leguminosae is considered as three distinct families, and there is a predominance of climbers in the Bignoniaceae (Peixoto and Gentry 1990).

Annual rainfall is quite low for a closed-canopy tropical moist forest, averaging 1,200 mm (measured from 1978 to 2000) with a pronounced dry season (defined as less than 50 mm month⁻¹) from May to

August and mean maximum and minimum average temperatures of 25.2 and 19.1°C. In the study area, the unusual strength of the 1987 and 1998 ENSO (El Niño Southern Oscillation) events is best illustrated by examining dry season rainfall (Fig. 2). During the dry season in these ENSO years, rainfall (May–August) was 23.2 mm (1987) and 31.3 mm (1998), or less than one-fifth of average precipitation. Moreover, in 1998 the drought continued into September, when precipitation was only 15 mm.

Plot description and census

A long-term experimental study of tree-community dynamics, biomass, and composition has been conducted in logged (since 1980) and unlogged forests (since 1978) in Vale do Rio Doce Reserve (Fig. 1). The objective of the experiment is to compare the effect of different partial cuttings on forest growth, yield, and species diversity. The experiment was installed using a completely randomized block design with nine treatments and five blocks. For this study, data were pooled from five 0.5-ha (100×50 m) permanent plots in unlogged sites (control). Following the initial census of all trees in 1978, each plot was recensused ten times (1983, 1986, 1989, 1992, 1993, 1994, 1995, 1997, and 1999) to assess tree mortality, recruitment, and growth, with a final census conducted in 2000. In each census, all trees ≥10 DBH were measured at 1.3 m height or above any buttresses.

Tree mortality and recruitment

For each census interval, we calculated mean annual rates of tree mortality as $m = 1 - [(N_0 - N_m)/N_0]^{1/t}$, and recruitment as $r = [(N_0 + N_r)/N_0]^{1/t} - 1$, where N_0 is the number of trees at the beginning of the interval, N_m and

Fig. 2 Dry season rainfall (May–August) at the Linhares Natural Reserve, Brazil, from 1975 to 2000. The severe drought (ENSO events) occurred in 1987 and 1998

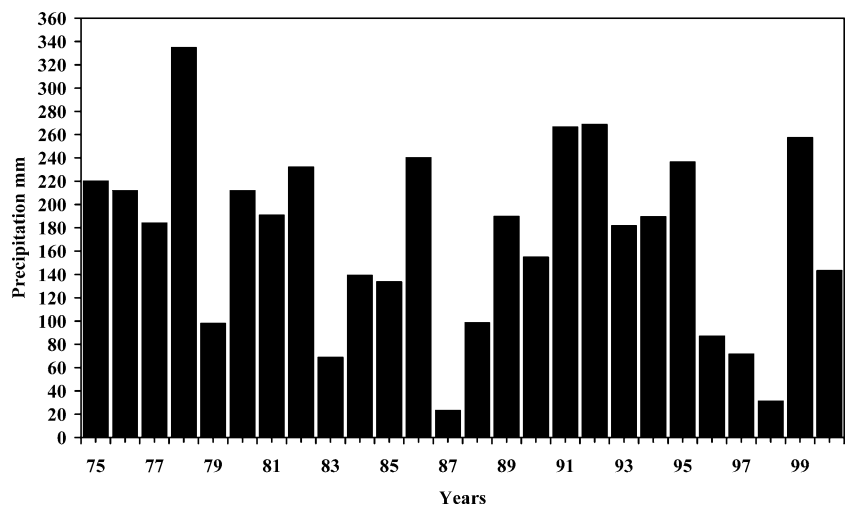


Table 1 Above-ground biomass (AGB_T), annualized mortality (m) and recruitment (r) rates, production of coarse wood debris (CWD), above-ground biomass change (ΔM_{stand}), and above-ground biomass increment (ΔM_I) over the 22-year period at Vale do Rio Doce Reserve

	1978	1983	1986	1989	1992	1993	1994	1995	1997	1999	2000	Mean
AGB_T	340.9	367.1	379.2	314.5	327.7	332.7	333.6	334.2	333.4	306.1	309.8	334.5
r	–	0.8	1.2	2.3	2.3	2.4	2.4	1.3	1.1	1.7	5.1	2.1
m	–	0.7	1.4	3.8	0.9	1.4	1.6	1.0	1.7	4.9	2.4	2.0
CWD	–	2.1	3.5	27.5	2.5	1.9	3.7	2.6	2.7	17.4	5.5	6.9
ΔM_{stand}	–	4.8	4.0	–21.6	4.4	5.0	0.9	0.6	–0.4	–13.6	3.6	–1.2
ΔM_I	–	6.7	7.3	5.4	6.4	6.4	4.2	2.9	2.0	3.4	8.1	5.3

N_r are, respectively, the number of trees that died and recruited during the interval, and t is the number of years (Sheil and May 1996). To determine whether tree sizes are equally susceptible to droughts, we placed the distribution of trees dying in each census interval into four size classes (10–19.9, 20–39.9, 40–59.9, ≥ 60 cm).

Above-ground biomass estimates and production

Since specific allometric equations for our study were not available, DBH measures for each census and each plot were converted to above-ground dry biomass (AGB) estimates using an allometric equation given in Chave et al. (2001) for moist tropical forest. For each tree, AGB was calculated as: $\ln(AGB) = -2.19 + 2.54 (\ln DBH)$, where AGB is measured in kg (dry biomass) and DBH is in cm. Total biomass (AGB_T) for each plot and in each census was the sum of all individual live tree biomass.

Census data from the five permanent plots were used to estimate change in total stand mass ($\Delta M_{stand} = AGB_{t2} - AGB_{t1}$) and above-ground biomass increment ($\Delta M_I = AGB_G + AGB_R$) as describe in Clark et al. (2001b), where AGB_{t2} and AGB_{t1} are the above-ground biomass of live trees at time 2 and time 1, respectively, AGB_G is the above-ground biomass increment of all surviving tree between at the end and beginning of the interval, and, AGB_R is the biomass increment of recruitment. The increment of each new tree (AGB_R) is calculated as the difference between its estimated biomass at the end of the interval and the biomass of a tree of the minimum measured diameter (in this case = 10 cm DBH). We also computed coarse wood debris (CWD), the biomass of trees that died in the interval. For all variables, confidence intervals (95% CI) were calculated as the mean $\pm (t_{0.05}) \times$ mean standard error (Cochran 1977).

The variables CWD and AGB_T were analyzed using linear regression. Both minimum precipitation during the previous year (from May to August) and time (1978–2000) were used as independent variables. Although time is not an explanatory variable, it allowed for a visual interpretation of temporal tendencies in ΔM_I . We expected that the high CWD for the current year was primarily caused by minimum precipitation during the previous year(s), and that ΔM_I will be higher after

drought, balancing preceding losses. The univariate F -test was applied to CWD and ΔM_I to verify imbalances between census years and one-tailed paired t -tests were performed to compare CWD production in pre-ENSO and ENSO events (1983–1986 vs 1986–1989 and 1995–1997 vs 1997–1999). Biomass components with variances between census that were not homogenous according to the Hartley test ($P < 0.05$), and that did not exhibit a normal distribution (Shapiro-Wilks, $P < 0.05$), were transformed using a natural logarithm [$\ln(x + 1)$].

Results

Mortality and recruitment

Over the 22-year period, recruitment of new trees offset the losses caused by tree mortality. However, tree mortality was quite variable over the entire period, and substantially increased following droughts (1989 and 1999, Table 1). The mean mortality rate for 22-year period was 2.0% year⁻¹, but it was 1.4% when only non-ENSO intervals were used. On average, tree mortality during the 1986–1989 and 1997–1999 periods was nearly 3–4 times greater than the mean rate of non-ENSO intervals. Despite the variation in mortality among size classes during 1986–1989 interval, all classes showed increased mortality in both ENSO periods (Fig. 3).

Variation of aboveground biomass among plots and census

Total above-ground biomass ranged broadly from 241.2 to 436.9 Mg ha⁻¹ for all plots and census ($n = 5$ plots $\times 11$ censuses), averaging 334.5 Mg ha⁻¹ (± 11.3 , 95% CI) (Table 1). In the 1986/1989 (ENSO period) biomass was reduced by 17.1%. Although less severe, the 1998 drought also caused a decline in forest biomass, with a mean reduction of 8.2% of the total biomass. The high variation among plots and census (Fig. 4) was mainly due to the presence and absence of “giant” trees (≥ 100 cm DBH). Plots 3 and 4 had the highest biomass in the initial census, with three giant trees in plot 3 and four giant trees in plot 4. These trees comprised more than 9.3 and 15.8% of the total biomass in each plot,

Fig. 3 Size distribution of dead trees for all census intervals

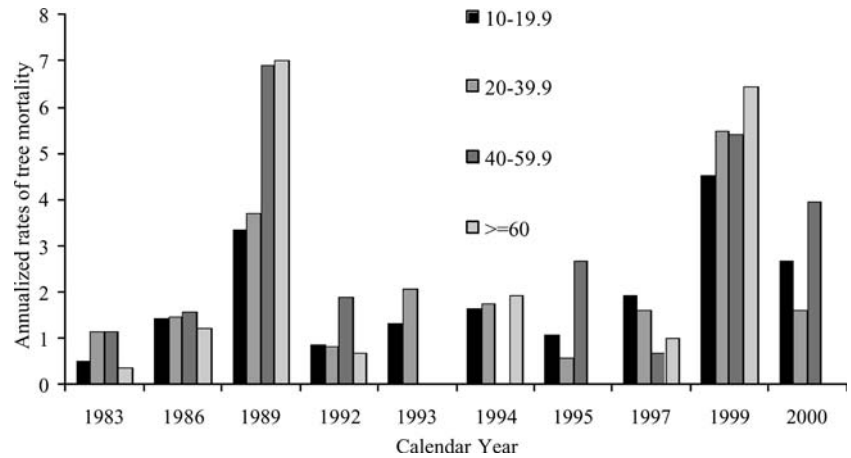
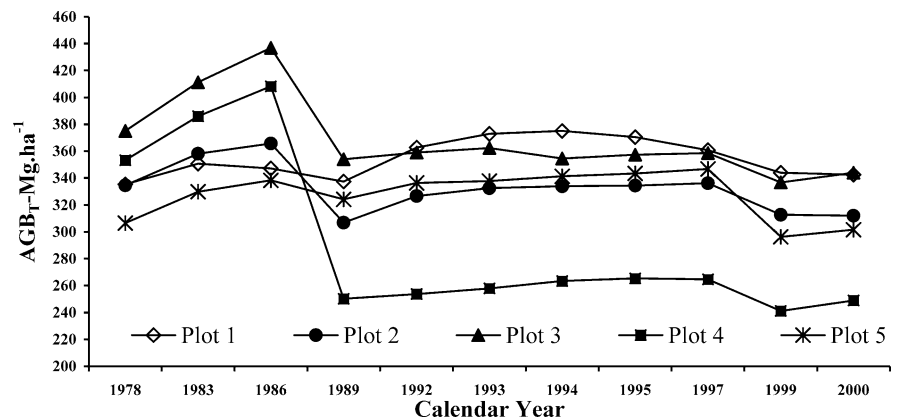


Fig. 4 Above-ground biomass (AGB_T) for each 0.5-ha plot and over the 1978–2000 study period at the Linhares Atlantic forest. Decreasing in above-ground biomass was significant between 1978 and 2000 ($F=9.5$, $P<0.003$, $R^2=0.15$)



respectively, in 1986. During the 1986–1989 interval (after the 1987 drought), 42.7% of total CWD across all 2.5 ha occurred in plot 4, because three giant trees died (92.6% of biomass death in plot 4), while 24.4% of total CWD across all 2.5 ha occurred in plot 3, with a death of one giant tree (34.8% of biomass death in plot 3). No giant trees died during the 1997–1999 interval, which in large part explains why the second ENSO event had less impact on total forest biomass. In contrast, during the years between droughts (1989 and 1997) AGB_T increased slightly (Fig. 4), but there was a significant decrease in AGB_T over the entire census period ($F=9.5$, $P<0.003$, $R^2=0.15$).

Aboveground biomass change

As expected, post-drought CWD productions were more than 2–4 times the average rate (6.9 ± 3.0 $Mg\ ha^{-1}\ year^{-1}$). As a consequence, annual CWD input was highly variable among years ($F=6.6$, $P<0.0001$, $df=9$), ranging from 2.1 to 27.5 $Mg\ ha^{-1}\ year^{-1}$ (Table 1). In fact, CWD production in periods preceding ENSO events (1983–1986 and 1995–1997) were signifi-

cantly lower than those from ENSO periods (1986–1989 and 1997–1999; one-tailed paired t -test, $P<0.05$ for both cases).

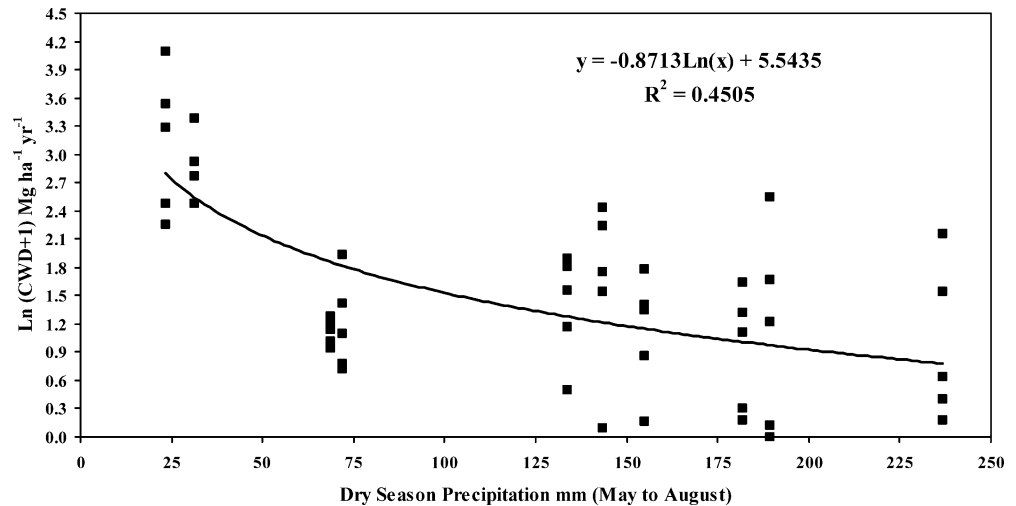
A scatter plot of annual CWD production and dry-season precipitation (Fig. 5) shows that year-to-year variability was related to the quantity of rain. In the years of high CWD production, ΔM_{stand} was largely negative, but before and after droughts, it was generally positive. Nevertheless, the 22-year average ΔM_{stand} was $-1.2\ Mg\ ha^{-1}\ year^{-1}$ (± 3.1) (Table 1). ΔM_I was quite variable among years ($F=9.3$, $P<0.0001$, $df=9$) and averaged $5.3\ Mg\ ha^{-1}\ year^{-1}$ (± 0.7) for the entire period (Table 1). Although there were no clear environmental factors that accounted for ΔM_I variability, there appeared to be a pattern, with all plots showing declines in some particular years.

Discussion

Above-ground biomass

Total above-ground biomass (for trees ≥ 10 cm DBH) for tropical forests varies from less than 200 to more

Fig. 5 CWD as a function of dry-season (May–August) precipitation (precipitation < 50 mm corresponds to severe ENSO events)



the 400 Mg ha⁻¹ (Clark et al. 2001a). Various factors can be involved in this variability, with water availability among the most important (Clinebell et al. 1995; Baker et al. 2003). Yet despite the fact that the Linhares Reserve region received considerably less precipitation (1,200 mm year⁻¹ from January 1975 to December 2000) than most other tropical forest regions, and that ENSO events have a much larger relative effect on annual precipitation, AGB_T estimates from the data presented here (334.5 ± 11.3 Mg ha⁻¹) are quite similar to other tropical forests with greater annual precipitation.

Although our study presents a long detailed temporal scale, it may have failed to take into account the spatial variability of biomass because of its small sample size. The 2.5 ha sampled in this study is smaller than the 6–10 ha proposed by Chave et al. (2003) as the minimum area for accurate estimates of biomass stock in tropical forests. However, AGB_T in this 2.5-ha study was quite similar to values encountered in 250 plots of 20×80 m (40-ha averaging 332.8 Mg ha⁻¹ surveyed in RVRD in 1991, Jesus and Rolim 2004), demonstrating that plot bias was not responsible for our large forest biomass estimate. Our mean AGB_T was calculated using an 11-member temporal series, encompassing two periods with extreme ENSO events (1987 and 1998), which greatly intensified regional drought and tree mortality rates (Rolim et al. 1999). The considerable spatial variability among plots observed in this study is common for tropical forests, and caused by factors such as variability in soil characteristics, species composition, micro-topographic variability and differences in disturbance regimes (Saldarriaga et al. 1988; Clark et al. 1998; Laurance et al. 1999; Chave et al. 2001). In the area studied there is little topographic variability, and no significant differences in soil properties were found in five plots (Jesus 2001). The largest part of the variability among the plots was due to the occurrence of giant trees, such as found in others studies (Brown et al. 1995; Nascimento and Laurance 2002).

Tree mortality and recruitment

The mean mortality rate (2.0% year⁻¹) is within of range of 1.0–2.0% measured for tropical sites (Swaine 1989; Hartshorn 1990; Phillips and Gentry 1994; Lugo and Scatena 1996; Phillips 1996). Elevated recruitment rates after catastrophic disturbance are also reported for tropical forests (Lugo and Scatena 1996; Condit et al. 1996), and should likewise contribute to balancing out the naturally high mortality rates. As shown here, canopy and emergent trees experienced higher mortality than smaller trees during the 1987 drought. The same pattern was found after droughts in other tropical sites (Leighton and Wirawan 1986; Condit et al. 1995; Clark and Clark 1996). It is noteworthy that the ENSO effects occurred in all tree size classes—not just those with giant trees—and were evident during both the 1987 and 1998 events. However, the 1998 ENSO event may have had less impact on forest biomass because most drought-susceptible large trees died during the 1987 event.

Surprisingly, there was no apparent effect of the 1983 ENSO on tree mortality and biomass in our study area. Other research suggests that the 1983 ENSO did increase tree mortality in a neotropical forest in Panama (Condit et al. 1995, 1996), but for central Amazon forests, the 1983 ENSO appeared to produce less severe drought with only minor effects on forest dynamics (Williamson et al. 2000; Laurance et al. 2001). There is one plausible reason for this finding. The 1983 dry season precipitation was 68.7 mm, which is relatively high to be considered a severe drought, compared to 23.2 and 31.3 mm of rainfall in 1987 and 1998, respectively.

In this study, the drought-year mortality increases from 1.4 to 3.8 and 4.9% represent a magnitude of increase of 2.4 and 3.5% in 1986–1989 and 1997–1999 intervals, respectively. These values are much higher than 0.77% increase found in Panama in 1982–1985 ENSO interval compared to 1985–1990 post-drought interval (Condit et al. 1995) and 0.79% for central Amazon in 1997–1998 drought (Williamson et al. 2000).

This finding is unexpected considering that such semi-deciduous forests, with many water-stress resistant tree species, would be less susceptible to droughts than the rain forests in the Amazon and Panama.

Biomass change

Estimates of ΔM_I in mature tropical forests presented by Clark et al. (2001a) range from 0.6 Mg ha⁻¹ year⁻¹ in Hawaii to 7.6 Mg ha⁻¹ year⁻¹ on the Ivory Coast. Our result for a plateau forest along the Atlantic coast of Brazil (5.3 Mg ha⁻¹ year⁻¹) is within this range, although the negative value for average ΔM_{stand} (-1.2 Mg ha⁻¹ year⁻¹) shows a deficit in biomass accumulation during the 22 years studied, which is driven by forest response to ENSO events.

To analyze this deficit of biomass accumulation we need to detail the biomass components involved. It is evident that higher mortality follows strong ENSO years (1987 and 1998), and there were differences provoked by ENSO years. Clark et al. (2003) found differences in tree growth rates at La Selva, Costa Rica, ostensibly caused by ENSO related effects of 1998. However, Nakagawa et al. (2000) found little evidence for negative ENSO effects on tree growth for surviving trees in Sarawak forests, which may have been the result of rapid recuperation of photosynthetic capacity for these trees in the months following the ENSO events.

Following a large reduction in forest biomass after the ENSO events, ΔM_I is generally greater than biomass lost from tree mortality, and the forest slowly accumulates lost biomass. Although not particularly clear in the data presented here (Table 1), Chambers et al. (2004b) found that, for a logged forest in the Central Amazon, surviving trees exhibit significantly higher growth rates following the death of nearby trees, and a post-ENSO increase in ΔM_I would accelerate biomass recovery rates. It appears that in the absence of another strong ENSO event, or other catastrophic disturbances, ΔM_I will continue to balance out the negative value for ΔM_{stand} (-1.2 Mg ha⁻¹ year⁻¹). Thus, we find that, at least in 22 years, the forest was quite resilient to large mortality events, with a rapid accumulation of lost biomass. Chave et al. (2003) also found evidence for rejecting the hypothesis that forests of Barro Colorado in Panama are long-term sinks for atmospheric carbon, finding a ΔM_{stand} of -0.39 Mg ha⁻¹ year⁻¹ in the period 1985–2000. In addition, Clark (2004) also found no net 4-year change (1997–2000) in estimated above-ground biomass across the old-growth forest at La Selva, Costa Rica.

These results do not accord with 38 plots (of 50) found by Phillips et al. (1998), which showed an accumulation of biomass for neotropical forests, and which also stimulated a debate about methodological questions involved in the analyses (Clark 2002; Phillips et al. 2002a; Baker et al. 2004; Lewis et al. 2004). Possible explanations for this biomass accumulation include

forests response to climate disturbances, CO₂ fertilization, and other local disturbances (natural and anthropogenic) (Fearnside 2000; Malhi and Grace 2000; Malhi et al. 2002; Chambers and Silver 2004).

ENSO effects on carbon balance

Despite the spatial variability, results demonstrate that it is important to measure temporal variability in ΔM_I , for which there is much less information in the literature, to obtain a representative average, and begin to understand factors accounting for tree growth variability. ENSO brings profound alterations in tropical forests dynamics, as much in Atlantic forests of Brazil as in other regions, including: the Amazon (Gale and Barford 1999; Williamson et al. 2000; Laurance et al. 2001), Central America (Leigh et al. 1990; Condit et al. 1992, 1995), Borneo (Leighton and Wirawan 1986; Aiba and Kitayama 2002) and Sarawak (Nakagawa et al. 2000).

Two propositions can be offered in relation to the effects of ENSO. First, if the frequency of ENSO increases as a result of climate change, changes in AGB may continue to be negative and many forests may enter into a biomass collapse dynamic, decreasing carbon stocks with the loss of large trees, similar to that which occurred in areas subject to fragmentation in the Central Amazon (Laurance et al. 1997; Nascimento and Laurance 2004). In this case an increase in ENSO frequency could limit, or perhaps even reverse any tendency of tropical forests toward biomass accumulation (Phillips et al. 1998). Second, if ΔM_{stand} approaches zero in the coming years, this would suggest that ENSO does not have a long-term effect on the biomass balance of the Linhares Atlantic forest and the forest is in a steady state dynamic with respect to biomass.

We find that in areas impacted by strong ENSO related mortality events, a biomass inventory carried out a few years after the event will contain considerably less biomass than an inventory carried out many years later. Over shorter time scales is entirely possible that increases in AGB_T will be due to temporary imbalances in the forest structure as a result of past disturbances, such as ENSO or other causes of elevated mortality (Fearnside 2000). For example, if we consider only the interval from 1989 to 1997 in Table 1 (8 years), a large increase in AGB_T from 314.5 to 333.4 Mg ha⁻¹ is demonstrated, and it could be concluded that the forest is accumulating significant biomass. Thus, depending on the timing and recurrence interval of disturbance events, biomass inventories, particularly those carried out over the short term, can give faulty conclusions concerning forest carbon balance.

Acknowledgements We are grateful to the Companhia Vale do Rio Doce for providing research support. We also thank C. Zartman and two anonymous reviewers for many constructive comments and suggestions on the manuscript, as well as all field technicians for their efforts.

References

- Aiba SI, Kitayama K (2002) Effects of the 1997–98 El Niño drought on rain forests of Mount Kinabalu, Borneo. *J Trop Ecol* 18:215–230
- Baker TR, Burslem DFRP, Swaine MD (2003) Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspect Plant Ecol Evol Syst* 6:21–36
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Killeen T, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patiño S, Pitman NCA, Silva N, Vásquez Martínez R (2004) Increasing biomass in Amazonian forest plots? *Phil Trans R Soc London B* 359:353–365
- Brown IF, Martinelli LA, Thomas WW, Moreira MZ, Ferreira CAC, Victoria RA (1995) Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. *For Ecol Manage* 75:175–189
- Chambers JQ, Silver WL (2004) Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Phil Trans R Soc London B* 359:463–476
- Chambers JQ, dos Santos J, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *For Ecol Manage* 152:73–84
- Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, dos Santos J, Araújo AC, Kruijt B, Nobre AD, Trumbore SE (2004a) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecol Appl* 14:72–88
- Chambers JQ, Higuchi N, Teixeira LM, dos Santos J, Laurance SG, Trumbore SE (2004b) Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* (in press)
- Chave J, Riera B, Dubois MA (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *J Trop Ecol* 17:79–96
- Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP (2003) Spatial and temporal variation in biomass of a tropical forest: results from a large census plot in Panama. *J Ecol* 91:240–252
- Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol Appl* 12:3–7
- Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Phil Trans R Soc London B* 359:477–491
- Clark DB, Clark DA (1996) Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *For Ecol Manage* 80:235–244
- Clark DB, Clark DA, Rich PM (1993) Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica* 25:397–407
- Clark DB, Clark DA, Read JM (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J Ecol* 86:101–112
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA. (2001a) Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecol Appl* 11:371–384
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001b) Measuring net primary production in forests: concepts and field methods. *Ecol Appl* 11:356–370
- Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc Natl Acad Sci USA* 100:5852–5857
- Clinebell RR II, Phillips OL, Gentry AH, Stark N, Zuuring H (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodivers Conserv* 4:56–90
- Cochran WG (1977) Sampling techniques. Wiley, New York
- Condit R, Hubbell SP, Foster RB (1992) Short-term dynamics of a neotropical forest. *Bioscience* 42:822–828
- Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical trees and shrub species and the impact of a severe drought. *Ecol Monogr* 65:419–439
- Condit R, Hubbell SP, Foster RB (1996) Changes in tree species abundance in a neotropical forest over eight years: impact of climate change. *J Trop Ecol* 12:231–256
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wsniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- Engel VL (2000) Estudo Fenológico de Espécies Arbóreas de uma Floresta Tropical em Linhares—ES. PhD Thesis, Campinas University
- Fearnside PM (2000) Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Clim Change* 46:115–158
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240
- Gale N, Barford AS (1999) Canopy tree mode of death in a western Ecuadorian rain forest. *J Trop Ecol* 15:415–436
- Garay I, Kindel A, Jesus RM (1995) Diversity of humus forms in the Atlantic forest ecosystems (Brazil): the tableland Atlantic forest. *Acta Oecol* 16:553–570
- Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre C, Moncrieff JM, Massheder J, Malhi Y, Wright IR, Gash J (1995). Carbon dioxide uptake by an undisturbed tropical rain forest in Southwest Amazonia, 1992–93. *Science* 270:778–780
- Hartshorn GS (1990) An overview of neotropical forest dynamics. In Gentry AH (ed) *Four neotropical rainforests*. Yale University Press, New Haven, pp 585–599
- IPCC (2001) Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the international panel on climate change. Cambridge University Press, Cambridge
- Jesus RM (2001) Manejo florestal: impactos da exploração na estrutura da floresta e sua sustentabilidade econômica. PhD Thesis, Campinas University
- Jesus RM, Rolim SG (2004) Fitossociologia da floresta atlântica de tabuleiro. *Boletim SIF* (in press)
- Laurance WF, Laurance SG, Ferreira LV, Rankin-de-Merona JM, Gascon C, Lovejoy TE (1997) Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118
- Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Rankin-de Merona JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *For Ecol Manage* 118:127–138
- Laurance WF, Williamson GB, Delamonica P, Oliveira AA, Lovejoy TE, Gascon C, Pohl L (2001) Effects of a strong drought on Amazonian forest fragments and edges. *J Trop Ecol* 17:771–785
- Leigh EG Jr, Windsor DM, Rand AS, Foster RB (1990) The impact of the “El Niño” drought of 1982–83 on a Panamanian semideciduous forest. In: Glynn PW (ed) *Global ecological consequences of the 1982–83 El Niño-Southern Oscillation*. Elsevier, Amsterdam, pp 473–486
- Leighton M, Wirawan N (1986) Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–83 El Niño Southern Oscillation event. In: Prance GT (ed) *Tropical forests and the world atmosphere*. West View, Boulder, pp 75–102
- Lewis SL, Phillips OL, Baker TR, Lloyd J, Malhi Y, Almeida S, Higuchi N, Laurance WF, Neill DA, Silva JNM, Terborgh J, Torres Lezama A, Vásquez Martínez R, Brown S, Chave J, Kuebler C, Núñez Vargas P, Vinceti B (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Phil Trans R Soc London B* 359:421–436
- Lugo AE, Scatena FN (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28:585–599

- Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Trends Ecol Evol* 15:332–337
- Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a Central Amazonian rain forest. *J Geophys Res D* 103:31593–31612
- Malhi Y, Meir P, Brown S (2002) Forests, carbon and global climate. *Phil Trans R Soc London A* 360:1567–1591
- Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorse CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–240
- Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T, Sato K, Miguchi H, Nagamasu H, Ogino K, Teo S, Hamid AA, Seng LH (2000) Impact of severe drought associated with the 1997–98 El Niño in a tropical forest in Sarawak. *J Trop Ecol* 16:355–367
- Nascimento HEM, Laurance WF (2002) Total above-ground biomass in central Amazonian rainforests: a landscape-scale study. *For Ecol Manage* 168:311–321
- Nascimento HEM, Laurance WF (2004) Biomass dynamics in Amazonian forest fragments. *Ecol Appl* 14:127–138
- Peixoto AL, Gentry A (1990) Diversidade e composição florística da mata de tabuleiro na Reserva Florestal de Linhares (Espírito Santo, Brasil). *Rev Bras Bot* 13:19–25
- Peixoto AL, Silva IM (1997) Tabuleiro forests of northern Espírito Santo, South-eastern Brazil. In: Davis SD, Heywood VH, Herrera-McBryde O, Villa-Lobos J, Hamilton AC (eds) *Centres of plant diversity: a guide and strategy for their conservation*, vol 3. The Americas, WWF/IUCN, Cambridge, pp 369–372
- Peixoto AL, Silva IM, Pereira OJ, Simonelli M, Rolim SG (2004) Tabuleiro forests north of the rio Doce: their representation in the Vale do Rio Doce Natural Reserve, Espírito Santo, Brazil. *Mem New York Bot Gard* (in press)
- Phillips OL (1996) Long-term environmental change in tropical forests: increasing tree turnover. *Environ Conserv* 23:235–248
- Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science* 263:954–958
- Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nunez PV, Vasquez RM, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442
- Phillips OL, Malhi Y, Vinceti B, Baker T, Lewis SL, Higuchi N, Laurance WF, Vargas PN, Martinez RV, Laurance S, Ferreira LV, Stern M, Brown S, Grace J (2002a) Changes in growth of tropical forests: evaluating potential biases. *Ecol Appl* 12:576–587
- Rolim SG, Chiarello AG (2004) Slow death of Atlantic forest trees in cocoa agroforestry in southeastern Brazil. *Biodiversity Conserv* (in press)
- Rolim SG, Couto HTZ, Jesus RM (1999) Mortalidade e recrutamento de árvores na floresta atlântica em Linhares (ES). *Sci For* 55:49–69
- Rolim SG, Couto HTZ, Jesus RM (2001) Fluctuaciones temporales en la composición florística del bosque tropical atlántico. *Biotropica* 33:12–22
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence in the upper rio Negro of Colombia and Venezuela. *J Ecol* 76:938–958
- Saleska SR, Miller SD, Matross DM, Goulden ML, Wofsy SC, da Rocha HR, de Camargo PB, Crill P, Daube BC, de Freitas HC, Hutya L, Keller M, Kirchhoff V, Menton M, Munger JW, Pyle EH, Rice AH, Silva H (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science* 302:1554–1557
- Sheil D, May R (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J Ecol* 84:91–100
- Swaine MD (1989) Population dynamics of tree species in tropical forests. In: Holm-Nielsen LB, Nielsen IC, Balslev H (Eds) *Tropical forests: botanical, dynamics, speciation and diversity*. Academic, London, pp 101–109
- Williamson GB, Laurance WF, Oliveira AA, Delamonica P, Gascon C, Lovejoy TE, Pohl L (2000) Amazonian tree mortality during the 1997 El Niño drought. *Conserv Biol* 14:1538–1542