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Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest

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Abstract

The loss of tree mass over time from damage can lead to underestimates in above-ground net primary productivity (ANPP) if not accounted for properly. Bias in the allometric relationship between trunk base diameter (D_b , at 1.3 m height or above the buttresses) and mass can also lead to systematic errors in ANPP estimates. We developed an unbiased model of the relationship between D_b and tree mass using data from 315 trees (≥ 5 cm D_b) harvested in the central Amazon. This model was compared with other theoretical ($n = 1$) and empirical models ($n = 4$). The theoretical model, and one empirical model, made predictions that differed substantially from our central Amazon model. The other three empirical models made predictions that were consistent with our model despite being developed in different tropical forests. Models differed mostly in predicting large tree mass. Using permanent forest inventory plot data, our D_b versus tree mass model, and a bole volume model, we estimated that tree damage amounts to 0.9 Mg ha⁻¹ per year (dry mass) of litter production. This damage should be included as a mass loss term when calculating ANPP. Incorporating fine litter data from published studies, we estimated that average ANPP for central Amazon plateau forests is at least 12.9 Mg ha⁻¹ per year (or 6.5 Mg C ha⁻¹ per year). Additional sources of error as described in the text can raise this estimate by as much as 4 Mg ha⁻¹ per year. We hypothesize that tree damage in old-growth forests accounts for a significant portion of age related decline in productivity. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Net ecosystem production; Carbon cycling; Tropical forest; Coarse wood litter; Tree mortality; Forest fragmentation; NPP

1. Introduction

Net primary production (NPP) is defined as the biochemical construction of new organic material over a specified time interval, or gross primary production (GPP) less autotrophic respiration. The NPP of an

ecosystem drives all heterotrophic activity (e.g. population and community dynamics), controls net ecosystem production (NEP) by sequestering atmospheric CO₂, and supplies organic material for heterotrophic respiration. Despite these key roles, NPP is notoriously difficult to quantify, especially for forests. Evidence is accumulating that tropical forests are sequestering carbon (Grace et al., 1995; Malhi et al., 1998; Phillips et al., 1998), conceivably brought about by CO₂ fertilization and a subsequent increase in NPP. Because changes in NPP can have global significance,

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and can change ecosystem structure and functioning (Mooney et al., 1996; Chapin et al., 1998), measures of NPP with a considerable degree of accuracy are needed. Uncertainty in NPP estimates for tropical forests are particularly large (Clark et al., 2000a).

To measure NPP, the production of new organic matter over a specified time interval is quantified. The stand mass increment (ΔM_i) primarily accounts for the production of long-lived tissues (stem wood and large branches), and is defined here as the change in mass of surviving trees in an inventory plot over time. Tree mass is best estimated using allometric relationships based on a representative harvest of trees where attributes of individuals (e.g. trunk base diameter, tree height, wood density) are correlated with mass. The production of short-lived material (fine litter; e.g. leaves, small stems, reproductive organs, etc.) is difficult to measure directly, and the death of these tissues is often used as a surrogate. Thus, above-ground NPP (ANPP) is often estimated as the sum of stand increment and litterfall rates, although other loss processes such as herbivory and the volatilization of organic molecules also factor in NPP estimates (Clark et al., 2000a).

When calculating ANPP, litter must be either new material that was produced and lost during the interval, or older material that was produced before, and lost during, the interval. Thus, considering an interval t_1 to t_2 , tree mass at t_2 is given by: $M_{t_2} = M_{t_1} - L_{old} + \Delta M_i$, where ΔM_i is the mass increment of all surviving trees, and L_{old} is mass present at t_1 , but lost by t_2 , as first detailed by Kira et al. (1967). Solving for the mass increment gives: $\Delta M_i = M_{t_2} - M_{t_1} + L_{old}$. This mass balance equation may appear counter-intuitive because it seems to imply that if M_{t_1} and M_{t_2} are equal, and L_{old} is positive, then trees gain mass by losing old organic material. However, if L_{old} is positive, then this mass must have been lost from M_{t_1} . Thus for M_{t_1} and M_{t_2} to be equal at t_2 , the trees must have gained in mass (i.e. produced) an amount equal to the losses. In a sense, not accounting for L_{old} results in underestimates by concealing production. Because most studies do not correct for L_{old} , to facilitate comparisons, we will refer to the measured stand mass increment as ΔM_i (i.e. $M_{t_2} - M_{t_1}$), and the loss corrected stand mass increment as ΔM_i^* (i.e. $M_{t_2} - M_{t_1} + L_{old}$).

Because litterfall includes both material already present at t_1 , and material produced and lost from t_1 to t_2 , a portion of the L_{old} term is accounted for by fine

litterfall. However, trees also lose previously accumulated mass as branch-fall, crown loss, and heart-rot (structural losses), and these losses are usually not considered. Also, because short-lived components such as leaves, fruits and flowers can be both produced and lost during the interval (L_{new}), and because it is difficult to separate old and new mass losses, a functional mass balance equation is given by: $ANPP = M_{t_2} - M_{t_1} + L$ (Eq. (1)), where L is both old and new losses, or all litter (coarse and fine).

Many tropical tree species have the capacity to survive stem breakage and crown loss. Negreros-Castillo and Hall (2000), for example, found that all 17 species they studied were capable of sprouting following an overstorey removal experiment in Quintana Roo, Mexico. Bellingham et al. (1994) found that 61.4% of 4949 trees had sprouts following a hurricane in a Jamaican montane rain forest, and Putz and Brokaw (1989) found that 41% of trees that sprouted following stem breakage in the period 1976–1980 were still alive in 1987 on Barro Colorado Island, Panama. Thus, the capacity to survive massive structural damage by sprouting is apparently widespread in tropical forests. Tree age and state of senescence is also extremely variable in tropical forests, with maximum age exceeding 1000 years (Chambers, 1998).

When harvesting for developing allometric models, trees should be selected regardless of the extent of damage, or state of senescence, otherwise total tree mass at the plot scale will be underestimated. Conversely, if trees with optimal structural characteristics are harvested for developing allometric models (cf. Clark and Clark, 2000), the correction for L_{old} (described above) will tend to overestimate productivity. Nevertheless, all trees lose mass as they grow in size by shedding branches, and to develop unbiased allometric relationships, and produce accurate productivity estimates, it is important to representatively sample the forest. Nevertheless, most allometric relationships are based on few harvested trees, and it is often unclear how trees were selected for sampling (Overman et al., 1994; Brown, 1997, and references therein).

In a review of tropical forest NPP estimates from 39 globally distributed sites (Clark et al., 2000b), none of the studies cited included an estimate of structural losses. To estimate structural losses, the rate of branch fall, crown loss, and heart-rot from surviving trees is required. This presents difficulties because most

damage probably occurs within large, relatively rare, tree-fall gaps, and there is little quantitative information on the extent of heart-rot in tropical forests (Brown et al., 1995).

The overall goal of this project was to quantify the effect of tree damage on ANPP estimates (Eq. (1)). The specific objectives were to (i) develop unbiased regression relationships (allometric models) for whole tree, bole and crown mass versus trunk base diameter; (ii) estimate stand mass, tree damage, and stand mass increment rates (Mg C ha^{-1} per year) using permanent forest inventory plot data; (iii) estimate average ANPP for dense central Amazon forests; and (iv) investigate sources of error introduced by use of different allometric models.

2. Materials and methods

2.1. Permanent forest inventory plots

Permanent forest inventory plots were established in the early 1980s by the Biomass and Nutrient Experiment (BIONTE), and the Biological Dynamics of Forest Fragments Project (BDFFP), in reserves of the National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazônia, INPA) in Brazil. Plots span an $20 \text{ km} \times 50 \text{ km}$ area about 60 km north of Manaus ($2^{\circ}30'S$, $60^{\circ}W$) in the central Amazon with an elevation of 50–150 m. Vegetation is old-growth closed-canopy tropical evergreen forest. Mean annual rainfall is 2200 mm and mean annual temperature is 26.7°C (National Climatic Data Center, Asheville, NC). The terrain is undulating, with soils comprising Oxisols on plateaus, Ultisols on slopes, and Spodosols associated with streams in small valley bottoms (Bravard and Righi, 1989). Surface (to 5 cm) clay content decreases ($\sim 75\text{--}5\%$), and sand content increases ($\sim 10\text{--}85\%$), when moving from plateau to valley (Ferraz et al., 1998). There is a distinct dry season during July–September with usually <100 mm of rain per month. A total of 1176 tree species have been identified in a nearby forest (Ribeiro et al., 1999).

2.2. Stand increment and allometric models

We developed allometric relationships based on 315 destructively sampled trees (hereafter referred to as

the “central Amazon allometry data”; Santos, 1996; Higuchi et al., 1998). All trees ≥ 5 cm trunk base diameter (D_b , defined as measured at 1.3 m or above the buttresses) were harvested from 0.2 ha subplot, randomly selected from a 1.0 ha plot located on a plateau (Oxisol) that was cleared for a biomass burning study (Carvalho et al., 1995). Bole and crown masses were tabulated separately, along with D_b . Regression analysis (SAS version 6.12) was used to determine unbiased (no trend in residuals) relationships between D_b and mass (whole tree, crown, and bole). The relationship between mass and D_b may be sensitive to the particular combination of trees harvested. To test this hypothesis we randomly divided the 315 trees into two groups, and predictions were compared.

Moisture content was measured for 50 of 315 sampled trees, in all components (e.g. bole, branches, leaves), with a mean and standard deviation of $0.38 \pm 0.08\%$ (normally distributed). To estimate dry mass for each harvested tree, we first assumed that moisture content was constant 38%. Next, to explore sensitivity of the allometric relationship to variation in moisture content, we assigned a random normal deviate from the moisture content distribution to each of the 315 tree masses, five separate times, and performed additional regressions. A comparison of regression parameters illustrated the sensitivity of dry mass estimates to variation in moisture content. Also, since selection of the 315 trees was not stratified by size (i.e. D_b), peculiarities in the small number of large trees harvested could have biased regression results. We tested for this effect by removing all trees >60 cm ($n = 8$) and re-doing the regression analysis.

Regression equations developed for different forests can give predictions that vary (Clark and Clark, 2000). To explore the applicability of models developed elsewhere, we compared mass predictions for the 315 harvested trees using five models (dry mass estimates): (1) derived from the theoretical work of West et al. (1997), and Enquist (personal communication), ($\ln[\text{mass}] = -2.30 + 2.67 \ln[D_b]$); (2) the tropical moist forest model of Brown (1997) ($\text{mass} = 42.7 - 12.8D_b + 1.24D_b^2$); (3) the tropical wet forest model of Brown (1997) ($\text{mass} = 21.3 - 6.95D_b + 0.74D_b^2$); (4) from a superhumid forest near Araraucua, Colombia (Overman 1994, $\ln[\text{mass}] = -1.97 + 1.24 \ln[D_b^2]$); (5) and an equation we developed from 127 trees harvested from a drier forest in the Eastern

Amazon (Araújo et al., 1999; $\ln[\text{mass}] = -6.03 + 5.03 \ln[D_b] - 0.372 \ln[D_b^2]$).

2.3. Quantifying tree damage

Structural wood loss was estimated using field notes taken during BDFFP forest inventories (17 ha). Living trees with snapped crowns and stems were documented in field notes, including the height where the stem snapped. New damage was estimated by comparing two consecutive inventories. A bole volume model based on the stem analysis of 288 trees (Ribeiro, 1996) was used to estimate the stem loss fraction

$$V_s = 0.0011 D_b^{1.8516} H_c^{0.9053} \left((H_c + H_s)^{0.118} - H_c^{0.118} \right) \quad (1)$$

where H_c is the height of the crown base, H_s the height of the snapped stem, and V_s is the volume left standing. The total volume (V_t) of the intact bole was calculated by substituting H_c for H_s (i.e. $H_c + H_s$ becomes $2H_c$) and the stem lost fraction was calculated using $(V_t - V_s)/V_t$. Separate regressions of D_b versus crown mass and D_b versus bole mass were used to calculate crown mass and the mass of the stem lost portion. Severely damaged crowns, as identified in the field notes, were assumed to be a 50% of loss of total crown mass. The loss of individual branches was not quantified.

2.4. Stand mass, mass increment, and ANPP estimates

Census data from 21 1 ha permanent plots from the BIONTE and BDFFP projects were used to estimate above-ground stand mass and stand mass increment (ΔM_i) for all trees with $D_b = 10$ cm. Data from published studies for comparable nearby forests (Klinge and Rodrigues, 1968; Franken et al., 1979; Luizão and Schubart, 1987; Sizer, 1992; Luizão, 1995), were used to estimate the fine surface litter portion of ANNP.

3. Results

3.1. Allometric models

Residual analysis demonstrated that a log–log-linear relationship with the central Amazon data

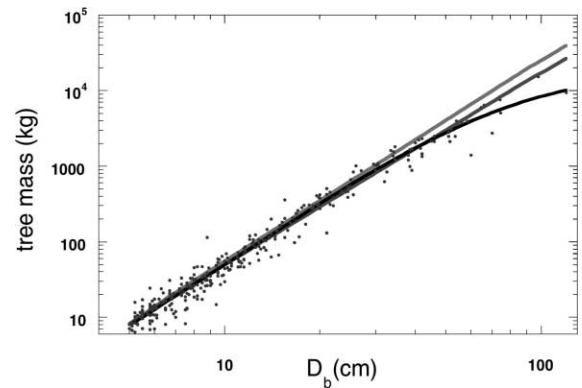


Fig. 1. Comparison of theoretical (light line), log–log-linear (darker line), and log–log-cubic (darkest line) relationships for the 315 harvested trees from the central Amazon. Apparently small differences in the shapes of these curves resulted in large differences in mass based predictions, especially for the largest trees (Table 3).

was biased toward overestimating stand mass by 5.6%. Bias increased with D_b , where the predicted mass of a 100 cm tree was overestimated by 101%. An unbiased model (hereafter referred to as “our model”) of mass versus D_b followed a log–log-cubic relationship (Fig. 1 and Table 1). All predictor variables were highly significant ($P_{\ln(D_b)} < 0.0001$, $P_{[\ln(D_b)]^2} < 0.0001$, $P_{[\ln(D_b)]^3} < 0.0001$). Separate regressions were highly significant for bole and crown masses versus D_b , although there was considerably more unexplained variability with crown mass versus D_b . Comparing the shape of the mass versus D_b relationship with the eastern Amazon data (Araújo et al., 1999), also demonstrated a curvilinear relationship on log–log transformed axes (Table 1). However, the eastern Amazon data included only trees ≥ 10 cm D_b , and an unbiased relationship followed a log–log-quadratic model, as compared with log–log-cubic model for central Amazon trees ≥ 5 cm. Regression analysis of the central Amazon data ≥ 10 cm D_b ($n = 161$) also followed a log–log-quadratic relationship (Table 1 and Fig. 2).

Results from the five moisture-error regressions demonstrated that variation in water content had little effect on the amount of unexplained error (Table 1). Applying the five regressions accounting for moisture variation, average prediction error for individual trees increased by 0.6–2.9%, and for the combined mass of

Table 1

Regression parameters for models with the general form: $\ln(\text{mass}) = \alpha + \beta_1 \ln(D_b) + \beta_2 [\ln(D_b)]^2 + \beta_3 [\ln(D_b)]^3$ for the 315 trees harvested in the central Amazon (mass in kg dry weight, D_b in cm)^a

Model	Parameter				Root			n
	α	β_1	β_2	β_3	r_{adj}^2	MSE	F	
Whole tree	-0.370	0.333	0.933	-0.122	0.973	0.297	3710	315
Whole tree linear	-2.010	2.550	n/a	n/a	0.970	0.310	10190	315
Whole tree >10 cm D_b	-4.898	4.512	-0.319	n/a	0.950	0.354	1166	161
Bole	-1.641	1.268	0.633	-0.093	0.964	0.336	2811	315
Crown	0.235	-1.713	1.588	-0.183	0.877	0.693	741	315
Moisture error	-0.161	0.071	0.912	-0.119	0.965	0.316	2931	315
	-0.425	0.405	1.041	-0.135	0.969	0.339	3259	
Trees <60 cm D_b	0.720	-1.042	1.467	-0.188	0.970	0.289	3324	307
Divided	-1.026	0.976	0.735	-0.103	0.972	0.313	1832	157
Moist forest	-1.335	1.551	0.415	-0.053	0.965	0.345	5655	611

^a The moisture error model shows the range in parameter estimates for five error simulations. “Divided” was a separate regression for half of the 315 harvested trees. The moist forest model was developed using all moist forest harvest data as described in the text.

all 315 trees (total mass) by 0.7–2.3%. Also, the largest trees did not have much influence on the shape of the regression relationship. Regression analysis for trees <60 cm D_b still followed a log–log–cubic form (Table 1), and predicted total mass was 15% less than the regression based on all trees. Likewise, the unique

combination of trees harvested had little effect on the relationship between D_b and tree mass. Using the regression derived from a random sample of half of the 315 trees (group 1), error in predicting individual tree mass (\pm S.D.) averaged $22 \pm 25\%$ for group 1 and $24 \pm 25\%$ for group 2 (the other half). Error predicting total mass was 8.7% for group 1 and 9.2% for group 2. Results were similar when the regression from group 2 was applied to group 1.

With the exception of (1) and (3) (Table 2), all models gave similar predictions for the mass of the 315 trees. Model (1), the theoretical model (West et al., 1997), assumes perfect, undamaged trees (B. Enquist, personal communication). This model was reasonable at predicting the mass of small trees, but greatly over-predicted the mass of large trees. The wet forest model (3) of Brown (1997) predicted tree mass for all size classes considerably lower than the other models. This was not simply because the model was developed in a wet tropical forest and applied to a moist forest (sensu Holdridge, 1967). The Overman et al. (1994) model (4), for example, was also developed in a wet tropical forest, and gave predictions consistent with tropical moist forest models. The largest differences among models was predicting mass of very large trees (Table 2). Our model was the most conservative in estimating large tree mass, and models (1) and (4) the most generous. Combining the central Amazon data, all tropical moist data from Brown (1997), and data

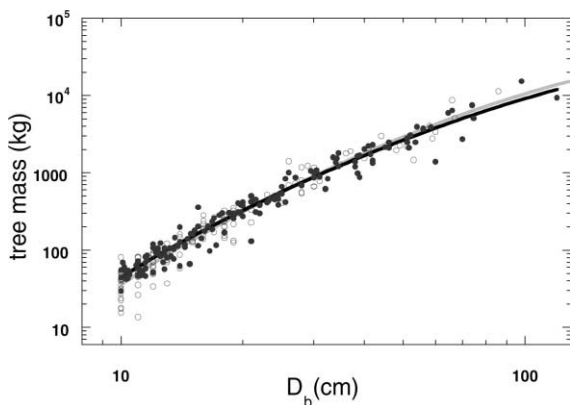


Fig. 2. The relationship between tree mass and D_b for two Amazon sites. Differences in both slope ($P = 0.0047$) and intercept ($P = 0.0011$) were significant between sites. Small trees in the eastern Amazon (light line, open circles) were slightly less massive, and large trees more massive, than in the central Amazon (dark line, filled circles), although absolute differences were small (see text). However, D_b alone accounted for much more variability ($F = 5250$), than site ($F = 10.9$), or the interaction term ($F = 8.1$).

Table 2
Measured mass, predicted mass, and residuals for 315 destructively sampled trees used to develop the allometric models presented here using five different models (see Section 2 for equation descriptions)^a

DBH (cm)	<i>n</i> (trees)	Tree mass (Mg)	Model predictions						Sum of residuals					
			Our model (Mg)	Model 1 (Mg)	Model 2 (Mg)	Model 3 (Mg)	Model 4 (Mg)	Model 5 (Mg)	Our model (Mg)	Model 1 (Mg)	Model 2 (Mg)	Model 3 (Mg)	Model 4 (Mg)	Model 5 (Mg)
5–10	154	3.3	3.1	3.1	2.6	1.6	3.0	2.0	–0.1	–0.2	–0.7	–1.7	–0.3	–1.3
10–20	90	11.9	11.1	10.8	10.1	6.5	9.2	10.1	–0.8	–1.1	–1.8	–5.4	–2.7	–1.7
20–30	28	14.3	13.4	13.2	12.3	7.7	10.3	13.6	–0.9	–1.1	–2.0	6.6	–4.0	–0.7
30–40	18	21.8	21.6	23.0	19.5	11.9	16.7	22.4	–0.2	1.2	–2.3	–9.8	–5.0	0.6
40–50	9	17.9	17.7	20.4	16.0	9.8	14.3	18.5	–0.2	2.5	–1.9	–8.1	–3.6	0.6
50–60	8	24.7	24.8	32.7	23.3	14.1	22.0	26.5	0.1	8.0	–1.4	–10.6	–2.7	1.8
>60	8	54.1	47.4	103.0	57.0	34.3	63.3	56.3	–6.7	48.9	2.9	–19.8	9.2	2.2
Sum	315	147.9	139.2	206.2	140.7	85.9	138.8	149.5	–8.7	58.2	–7.2	62.0	–9.1	1.5
150			11.8	63.8	26.1	15.6	35.6	18.9						
200			12.6	137.4	47.2	28.2	72.8	26.7						

^a Predictions for 150 and 200 cm D_b are provided to demonstrate model divergence for the largest trees.

from Araújo et al. (1999) produced a general tropical moist forest allometric model for predicting tree mass from D_b and also demonstrated a significant log–log–cubic relationship (Table 1).

3.2. ANPP estimates

The average stand mass increment (ΔM_i) ($\pm 95\%$ CI) estimated using our model was $3.9 (\pm 0.2) \text{ Mg ha}^{-1}$ per year for the BDFFP data, $5.5 (\pm 1.2) \text{ Mg ha}^{-1}$ per year for the BIONTE data, and $4.1 (\pm 0.3) \text{ Mg ha}^{-1}$ per year for both sites combined. The difference in stand increment between the BIONTE and BDFFP plots was highly significant ($P < 0.0001$). Stand mass ($>10 \text{ cm } D_b$) did not differ between sites ($P = 0.11$) and averaged $324 (\pm 17) \text{ Mg ha}^{-1}$ (Table 3). Structural wood lost for 17 ha of forest averaged $0.9 (\pm 0.2) \text{ Mg ha}^{-1}$ per year, and varied from 0.3 to 1.6 Mg ha^{-1}

per year (Table 4). Damage was partitioned into partial stem loss (57%), crown loss (37%), and partial crown loss (6%). Thus, corrected stand mass increment (ΔM_i^*) accounting for damage was 4.8 Mg ha^{-1} per year for BDFFP, 6.4 Mg ha^{-1} per year for BIONTE, and averaged 5.0 Mg ha^{-1} per year. Fine surface litter production at or near the BDFFP and BIONTE projects has been estimated at 7.3 Mg ha^{-1} per year (Klinge and Rodrigues, 1968), 7.9 Mg ha^{-1} per year (Franken et al., 1979), 8.3 Mg ha^{-1} per year (Luizão and Schubart, 1987), 8.4 Mg ha^{-1} per year (Sizer, 1992), and 7.8 Mg ha^{-1} per year (Luizão, 1995), averaging $7.9 (\pm 0.5, 95\% \text{ CI}) \text{ Mg ha}^{-1}$ per year. Accounting for stand mass increment, damage, and fine litterfall (Eq. (1)), average ANPP for central Amazon dense forests is estimated to be about 12.9 Mg ha^{-1} per year (dry mass), or 6.5 Mg C ha^{-1} per year.

Table 3

Stand estimates for 21 ha from BIONTE (B1S2, B2S3, and B4S5) and BDFFP (2302, 1202, 3402, and 3304) permanent plots for trees $>10 \text{ cm } D_b$ ^a

Site	Interval	Area (ha)	Number of stems (ha^{-1})	Stand mass (Mg ha^{-1})	Stand increment (Mg ha^{-1} per year)
2302	85–90	4	551	319	4.6
		5	550	311	4.1
		6	604	289	3.8
1201	81–91	1	529	328	4.0
		2	601	313	4.6
		3	550	297	3.9
3402	85–91	1	565	297	3.7
		2	562	297	4.0
		3	589	300	4.2
		4	617	306	3.9
		5	652	354	4.1
		6	719	353	3.6
		7	637	312	3.2
		8	626	325	3.7
		9	633	232	3.5
3304	84–92	6	641	367	3.7
		8	618	367	3.4
		9	682	373	3.9
B1S2	89–97	–	582	354	5.2
B2S3	–	–	714	391	6.1
B4S5	–	–	599	322	5.3

^a Stand increment estimates are statistically different ($P < 0.0001$) between BIONTE and BDFFP sites. Interval indicates years in which census were performed.

Table 4
Structural losses caused by tree damage for 171 ha plots from the BDFFP forest inventory plots^a

BDFFP site	Interval	Area (ha)	<i>n</i> (trees)	Rate (trees per year)	Rate (Mg ha ⁻¹ per year)
2302	87–90	4	20	6.7	0.72
		5	28	9.3	1.12
		6	13	4.3	0.50
1201	86–91	1	24	4.8	0.92
		2	11	2.2	0.52
		3	17	3.4	0.62
3402	88–91	1	9	3.0	0.93
		2	9	3.0	0.40
		3	14	4.7	1.16
		4	16	5.3	1.23
		5	24	8.0	0.99
		6	26	8.7	1.64
		7	11	3.7	0.63
		8	16	5.3	0.31
		9	21	7.0	1.07
3304	86–92	6	22	3.7	1.21
		8	29	4.8	0.79

^a Interval indicates years that census were performed.

4. Discussion

We have shown connections among developing allometric models, accounting for all litter losses, and providing accurate measures of ANPP. First, to develop unbiased allometric models for predicting stand mass, trees should be randomly selected for harvest. However, a random sample of trees in an old-growth tropical forest will include many that have lost structural mass due to damage, senescence, and branch shedding. Not only do these structural losses result in the production of litter (primarily coarse), but they can also conceal production if not accounted for because trees are simultaneously losing and gaining mass as they grow in size (see Section 1). We have demonstrated that massive structural damage alone (crown and partial trunk loss) accounts for a loss of 0.9 Mg ha⁻¹ per year in central Amazon forests, and this loss should be included in both ANPP and litter production estimates.

4.1. Allometric models

Interestingly, with the exception of models (1) and (3), relationships between tree mass and D_b developed

for different tropical forests were quite similar (Table 2). This suggests that constraints on the mass of a tree for a given stem diameter are similar for many tropical forests. In some cases this was true for both moist and wet (*sensu* Holdridge, 1967) tropical forests. The Overman et al. (1994) model (4), for example, was developed for a wet forest, and the relationship between tree mass and D_b was essentially identical to our model for trees <100 cm D_b . The wet forest model of Brown (1997) was an exception. This model was developed from trees harvested at three globally distributed sites: a lower montane forest in Puerto Rico (Ovington and Olson, 1970; site A), a montane forest in New Guinea (Edwards and Grubb, 1977; site B), and unpublished data near La Selva, Costa Rica (Joyce (1989); cited in Brown (1997); site C).

Multiple regression and ANOVA demonstrated that the relationship between tree mass and D_b for sites A and B was not significantly different. However, comparing sites A and B with all data from the moist forest sites demonstrated that tree mass for all D_b classes was much lower for sites A and B, than for all moist forest sites (*y*-intercept significantly different, $P < 0.001$; slope not significantly different, $P = 0.94$). Interest-

ingly, comparing site C with all moist forest data demonstrated that the mass of trees of small diameters were comparable, but large trees were much less massive (y -intercepts not significantly different, $P = 0.33$; slopes significantly different, $P < 0.0001$). Thus, when compared with the tropical moist forest data, trees from wet montane forest were less massive for all size classes, but trees from site C (wet lowland) were only less massive for larger size classes.

There are a finite number of plausible explanations for these differences in mass for a given D_b across tropical forest sites: (i) the relationship between D_b and height differs; (ii) damage rates vary; (iii) wood density varies; (iv) methodological differences or errors among studies; (v) or some combination of these factors. Perhaps trees in the montane forest sites (A and B) were stunted, and on average shorter for all diameter classes. Height data was not available in Brown (1997), so we could not test this hypothesis. For site C, which receives about 4000 mm per year (Clark and Clark, 1996), damage rates may be higher from more frequent storms and, on average, trees are losing mass from damage more rapidly as they increase in size. However, allometry is not invariably linked to climate because the tree mass versus D_b relationship from the other wet forest site (Overman et al., 1994) was similar to tropical moist forest. Wood density varies among and within species (Williamson, 1984; Reyes et al., 1992; Fearnside, 1997) and with elevation (Wiemann and Williamson, 1989), and may also play a role in site specific allometry.

The largest difference between models was predicting the mass of large trees (Table 2). For example, the predicted mass for a 2 m D_b tree among all models varied from 12.6 (our model) to 137.4 Mg (model 1). The theoretical model (1) assumes perfect, undamaged trees, although it is surprising that estimates diverged by an order of magnitude. Model 4 was developed for a wet forest in the western Amazon, and made the second highest prediction (72.8 Mg), whereas the other wet forest model (3) gave a considerably lower prediction (28.2 Mg). This disparity among models probably exists, at least in some part, because very few of the largest trees have been harvested for allometric studies. It is also important to note that trees >1 m D_b are rare in central Amazon forests, and that although the models differ widely in mass predictions for the largest trees, stand

estimates were quite comparable for most of the models compared here (Table 3).

Estimating the mass of large trees accurately is more critical when quantifying processes that have disproportionate effects on large trees. For example, (Laurance et al., 1997) demonstrated that forest fragmentation increases tree mortality near edges, and Laurance et al. (2000) further demonstrated that mortality for trees ≥ 60 cm D_b was almost 40% higher than for other size classes. We compared the log–log–linear and log–log–cubic regressions (Table 1) for trees ≥ 60 cm D_b from the BDFFP data (18 ha, $n = 167$) and found that the former overestimates ≥ 60 cm D_b mass by about 54% (1397 Mg versus 908 Mg). Predictions from our log–log–cubic model were not simply an artifact of the influence of the small number of large trees harvested; when we removed trees ≥ 60 cm D_b from the analysis, predicted mass for the largest trees was *less* than predicted from the model based on all 315 trees, and still followed a log–log–cubic relationship (Table 1).

As trees grow in size, change in mass for a given change in D_b increases more slowly than would be expected from a power-law relationship (e.g. West et al., 1997). This was demonstrated in both the central and eastern Amazon data (Figs. 1 and 2). The combined tropical moist forest dataset ($n = 611$, Table 1) also exhibited a log–log–cubic relationship, demonstrating that the phenomena of tree mass gain per unit D_b decreasing as D_b increases is widespread. Tree mass versus D_b starts out reasonably linear for small trees, and then begins to asymptote as trees grow beyond about 50 cm D_b (Fig. 1). This suggests that as trees increase in size, mass loss processes such as damage and senescence accelerate. If these loss processes were not prevalent, the relationship between D_b and mass would probably follow more closely the theoretical predictions of West et al. (1997).

4.2. ANPP estimates

Because a tree both loses and gains mass as it grows in size, if not accounted for, processes that reduce the mass of a tree over time lead to underestimates in ANPP. Here we estimated that tree damage amounted to 0.9 Mg ha⁻¹ per year. Since only massive structural loss was considered, and not individual branch loss, losses are underestimated. Van der Meer and Bongers

(1996), for example, found that 1.3% of trees in 12 ha of forests in French Guiana had lost at least one major branch over a year. Heartrot (the loss of heartwood from decomposition) is another structural loss term that should be considered. Brown et al. (1995) found that about 4% of the volume was hollow for stumps from 53 trees that were cut for a road clearing, although this sample was biased toward small stems. Accounting for heartrot will require large-scale (e.g. >10 ha) sampling, stratifying trees by D_b .

We refer to our ANPP estimate for central Amazon forest as an average. This is because ANPP studies that incorporate litterfall (coarse and fine) include old losses (L_{old} , see Section 1), and the productivity that accounts for these losses may or may not have occurred during the interval. For example, there are occasional years where tree damage rates are probably higher than average (Condit et al., 1995), and these elevated damage years are not necessarily coincident with an increase in productivity. However, average litter (coarse and fine) production rates measured over a number of years will tend to coincide with the total production of these tissues, and with the mass versus D_b relationship derived from a representative harvest of trees. However, ANPP estimates that incorporate litterfall rates cannot be used to assign productivity to particular years because a portion of the losses (primarily coarse litter) are old (L_{old}). It is worth noting that the tree mass increment (ΔM) can be assigned to particular years because it measures wood production (~98% of the mass of a tree) directly.

We must make a distinction between stand mass increment (our ΔM_i) and a change in total stand mass ($\Delta M_{stand} = \text{recruitment} + \Delta M_i - \text{mortality}$) as utilized, for example, in Phillips et al. (1998). Phillips et al. (1998) used changes in basal area to predict changes in total stand mass, and found that stand mass is increasing in mature Neotropical forests. A change in stand mass, however, is not the same as productivity. High mortality, for example, can lead to negative ΔM_{stand} , whereas NPP must always be ≥ 0 . Also, an increase in stand mass does not necessarily mean a change in productivity. A constant (or even declining) productivity can lead to an increase in ΔM_{stand} if not offset by mortality.

A number of other factors are important for developing precise and accurate estimates of ANPP. For example, Edwards (1977) found that small wood litter

lost an average of 36–40% of its mass before falling into litter traps. Frangi and Lugo (1985) found a similar decomposition loss by leaves trapped in the canopy before falling. If this extent of pre-trap decomposition is true for most litter, the ANPP estimates presented here would have to be corrected by a substantial 3 Mg ha^{-1} per year. Organic matter lost to herbivory can also be substantial (12–30%; Clark et al., 2000b; and references therein), although some portion of losses to herbivores is accounted for by insect remains caught in litter traps. Assuming that unaccounted for herbivory is 10% of forest leaf mass, this loss would amount to approximately 1 Mg ha^{-1} per year. Yet another issue is the growth of trees that die during the census interval. Assuming 2% per year stem mortality, for census intervals that are short (e.g. <5 years) such as in this study (Tables 3 and 4), this error probably accounts for <10% of the stand mass increment. There are also other factors that contribute toward developing precise and accurate estimates of ANPP that are difficult to account for quantitatively (Clark et al., 2000a).

A number of studies have demonstrated a decline in forest productivity with age (Gower et al., 1996). Mechanisms to explain this decline have focused on physiological factors such as increased respiratory costs for larger trees, age related decline in meristematic growth, and hydraulic limitations (Ryan and Yoder, 1997). A decline in productivity with age may explain some of the differences between the theoretical and empirical allometric relationships (Fig. 1). However, a portion of the decline may be also be caused by damage. As forests age, a larger proportion of the trees will have suffered damage events. Damage may also limit future productivity by reducing crown area and canopy photosynthetic capacity, and by exposing live tissues to infection by pests and pathogens, which can exacerbate senescence processes. We hypothesize that an increase in the fraction of damaged and senescent trees as forests age is an important contributor to age related decline in productivity.

Stand mass increment estimates from different projects in similar forests located within <100 km of each other (BDFFP and BIONTE) can exhibit significant differences (Table 2). It is not clear what accounts for these differences. The BDFFP plots had the advantage of a larger sample size, but the BIONTE project had

the advantage of a finer temporal resolution (i.e. plots measured every year for BIONTE as opposed to every 3–5 years for BDFFP) and it is easier to discover errors with many measurements for the same tree. Differences in mass increment estimates could be methodological, or reflect differences in site disturbance history, or other factors. Both studies measured D_b (i.e. above the buttresses), so methodological differences in how diameter was measured is probably not the cause. The average difference between these sites (1.6 Mg ha^{-1} per year) has a profound significance for the global carbon cycle, and for the structure and functioning of tropical forest ecosystems.

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