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Tree Height in Brazil's 'Arc of Deforestation': Shorter trees in south and southwest Amazonia imply lower biomass

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Abstract

This paper estimates the difference in stand biomass due to shorter and lighter trees in southwest (SW) and southern Amazonia (SA) compared to trees in dense forest in central Amazonia (CA). Because forest biomass values used to estimate carbon emissions from deforestation throughout Brazilian Amazonia will be affected by any differences between CA forests and those in the "arc of deforestation" where clearing activity is concentrated along the southern edge of the Amazon forest. At 12 sites (in the Brazilian states of Amazonas, Acre, Mato Grosso and Pará) 763 trees were felled and measurements were made of total height and of stem diameter. In CA dense forest, trees are taller at any given diameter than those in SW bamboo-dominated open, SW bamboo-free dense forest and SA open forests. Compared to CA, the three forest types in the arc of deforestation occur on more-fertile soils, experience a longer dry season and/or are disturbed by climbing bamboos that cause frequent crown damage. Observed relationships between diameter and height were consistent with the argument that allometric scaling exponents vary in forests on different substrates or with different levels of natural disturbance. Using biomass equations based only on diameter, the reductions in stand biomass due to shorter tree height alone were 11.0%, 6.2% and 3.6%, respectively, in the three forest types in the arc of deforestation. A prior study had shown these forest types to have less-dense wood than CA dense forest. When tree height and wood density effects were considered jointly, total downward corrections to estimates of stand biomass were 39%, 22% and 16%, respectively. Downward corrections to biomass in these forests were 76 Mg ha^{-1} (~ 21.5 Mg ha^{-1} from the height effect alone), 65 Mg ha^{-1} (18.5 Mg ha^{-1} from height), and 45 Mg. ha^{-1} (10.3 Mg ha^{-1} from height). Hence, biomass stock and carbon emissions are overestimated when allometric relationships from dense forest are applied to SW or SA forest types. Biomass and emissions estimates in Brazil's National Communication under the United Nations Framework Convention on Climate Change require downward corrections for both wood density and tree height.

keywords:
Allometry; Carbon; Global warming; Greenhouse gas emissions; Tropical forest; Wood density.

Introduction

Large scale patterns, such as physiognomy of the vegetation, floristic composition, tree turnover and biomass stock have recently been described for Amazonian vegetation (Eva et al., 2004; Houghton et al., 2001; Malhi et al., 2006; Phillips et al., 2004; Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006). Conventional classifications have generally assumed that the Amazon region has two main forest types, identified as "dense" and "open" forest (Veloso et al., 1991). The dense forest is more extensive (Brazil, IBGE, 1997) and has denser wood (Chave et al., 2006; Nogueira et al., 2005; Nogueira et al., 2007), giving this forest a larger biomass stock than open forest (Malhi et al., 2006). The per-hectare total basal area has been clearly shown to be higher in the central Amazon than at the region's southern edge, mainly due to the latter's abundance of small trees (Baker et al., 2004; Malhi et al., 2006). While dense forests are on poor soils, open forests occur on more fertile soils in the southern portion of Brazilian Amazonia (Brazil, RadamBrasil, 1973-1983; Brown and Prance, 1987; Malhi et al., 2004; Sombroek, 2000). Solar radiation is more seasonal and the dry season is longer in open forest, affecting tree species diversity and aboveground net primary productivity (Baker et al., 2004; Chave et al., 2006; Laurance et al., 2006; Malhi et al., 2004; Meinzer et al., 1999, 2001; ter Steege et al., 2003, 2006; Tuomisto et al., 1995).

Two open forest types disturbed by abundant lianas or climbing bamboo cover 366,000 km^2 of the southern Brazilian Amazon (Brazil, IBGE, 1997). Recent gaps and low-stature patches occupied 40% of a liana-dominated forest in the eastern Amazon (Gerwing and Farias, 2000). Forest dominated by climbing bamboo (*Guadua* spp.) is also largely composed of disturbed patches. These gap-rich forests sustain more fast-growing pioneer tree species. Consequently, wood density is lower than in neighboring dense forest without climbers (Nelson et al., 2006). In open forests disturbed by climbing bamboo or lianas (Schnitzer et al., 2000; Silveira, 1999; Putz et al., 1983; Putz, 1984), smaller trees suffer stem breakage and height loss (Clark and Clark, 2001; Griscom and Ashton, 2006). In the Peruvian Amazon, Griscom and Ashton (2006) found that, in the presence of abundant climbing *Guadua* spp., trees 5-29 cm in diameter attained an average height that was about 50-55% that of trees in the same size classes in nearby bamboo-free plots. Griscom and Ashton (2006) attributed this difference to crown and stem breakage. Trees larger than 30 cm dbh were mostly beyond the reach of bamboo and these showed no difference in average height between neighboring plots with and without bamboo. In a liana-dominated open forest in the Bolivian Amazon, Alvira et al. (2004) found that a large percentage of trees was infested in all dbh size classes, the largest trees having the highest frequencies and loads. Trees with lianas had more crown damage than trees without lianas.

Differences in the total height of trees are also expected among Amazonian forest types due to differences in ecological interactions, such as tree mortality, development of understory trees, competition and floristic composition, which affect vertical and horizontal structural patterns in forest canopies (Griscom and Ashton, 2003; Latham et al., 1998; Laurance et al., 2006; Lugo and Scatena, 1996; Muller-Landau et al., 2006; Weiner and Thomas, 1992). Thus, allometric relationships (such as the relationships among bole diameter, tree height, crown diameter and wood density) will be useful for understanding the structure and dynamics of tropical forests and the competitive interactions among the tree species (Bohlman and O'Brien, 2006; O'Brien et al., 1995; Perez, 1970; van Gelder et al., 2006; Weiner and Thomas, 1992). Furthermore, knowledge of variation in allometric patterns among Amazonian forests is likely to be useful in improving the underlying scaling relationships between diameter and tree size (Enquist, 1999, 2002; Muller-Landau et al., 2006; Niklas and Spatz, 2004).

Variation in the vertical structure of forests could directly affect biomass stock. In transition (open) forest, trees may be shorter at any given diameter as compared to trees in the dense forest in central Amazonia, and obviously the shorter of two stems of the same diameter will have less biomass. Similarly, lighter-density stems with the same volume have less biomass.

Recent Amazonian forest biomass studies applied wood density corrections and recognized the necessity of adapting allometry to improve biomass estimates, mainly at the southern edge of Amazonia (Baker et al., 2004; Malhi et al., 2004, 2006). However, if no correction is made for the height effect, the biomass will be overestimated by allometric relationships derived from central Amazonian studies. Recent wood density studies (Nogueira et al., 2007), combined with appropriate understanding of the structure of southern Amazonian forests, could provide substantial insights into the impact of land-cover and land-use change on the global carbon cycle. This is because the southern edge of Amazonia comprises the “arc of deforestation” and constitutes the predominant source of carbon emissions from deforestation in Brazil. This is also the area where the greatest uncertainties remain in carbon stock estimates (Houghton et al., 2000, 2001; Nepstad et al., 2001; Nogueira et al., 2007).

In this study we evaluate whether trees of southwestern and southern Amazonia forest are shorter at any given diameter than in central Amazonia. We also describe the scaling of tree stem diameter (D) with total height (L) in the four Amazonian forests studied. These were compared with the scaling relationship where log L is proportional to log $D^{2/3}$, which has been suggested as universal (e.g., West et al., 1999). In addition, we convert the differences in the total tree height and wood density between forest types into differences in estimates of stand biomass.

Materials and Methods

Study sites

At 12 sites in the Brazilian Amazon (in the states of Amazonas, Acre, Mato Grosso and Pará) 763 trees were measured (“diameter at breast height”, or dbh). Six sites were close to Manaus in central Amazonia (Nogueira et al., 2005) and the other six sites were distributed in the ‘arc of deforestation’: two sites in Acre state (SW open bamboo-dominated and SW dense forest), three sites in northwestern Mato Grosso state and one site in the southern portion of Pará state (together designated as “SA open forest”) (Nogueira et al., 2007). In each forest type, trees over 5 cm dbh were felled and measurements were made of total height, diameter (dbh or above buttresses) and wood density: 310 trees in CA dense forest, 92 trees in SW open bamboo-dominated forest, 97 trees in SW dense forest without bamboo and 264 trees in SA open forest (in this last forest type, wood density samples were taken from 72% of the trees).

Detailed descriptions of all sites are available in Nogueira et al. (2005, 2007). These two previous studies address the wood density effect on biomass and on estimates of carbon emissions based on wood volume inventories throughout Amazonia. In the present study the effect of the total height of trees, together with the previously published wood density dataset, are used to adjust allometric equations from well-studied forests in central Amazonia to the forests of southern and southwestern Amazonia, similar to recent studies that applied only wood density adaptations to allometric equations (Baker et al., 2004; Malhi et al., 2006).

Data collection

At all sites, trees to be felled were chosen randomly, but stratified by size classes starting at 5 cm dbh, according to the proportion that each class contributes to basal area in local forest inventories. For each tree, measurements were made of dbh (~1.36 m above the ground at the central Amazonia sites and 1.30 m above the ground at the other sites, or above buttresses when present for all sites), and total height. The wood density datasets used in this study were obtained from Nogueira et al. (2005, 2007), where detailed information is given on botanical specimens and the methodology for wood density determination.

Adapting allometry

Height × diameter relationship: effect on biomass

A combined analysis considering data on dbh-height allometries for the four forest types as one set, with forest type as a factor, showed that there was no significant difference ($p < 0.005$, post-hoc Bonferroni). Subsequently, the data from the two southwestern and the combined southern Amazonia forests (no difference between sites, $p = 0.390$) were compared with those from the central Amazon in paired regressions. Data for each pair were pooled so as to examine the effects on total tree height of ln(diameter), forest type and the interaction between ln(diameter) and forest type. If the interaction is significant (different slopes), the two regressions in a pair are different. If the interaction is nonsignificant, the two slopes are homogeneous and an analysis of co-variance is needed to test for a difference between the two intercepts. If the intercepts are different, a height correction can still be applied to the biomass. If neither the slopes nor the intercepts are different, the trees in the test forest and in the central Amazon forest are not distinguishable (Neter and Wasserman, 1974; Sokal and Rohlf, 1995). Only the effect of a shorter trunk is considered, including the portion inside the crown. The trunk is taken to be 66% of total tree biomass in central Amazonian dense forest (Higuchi et al., 1998). Percent biomasses of branches, twigs and leaves are assumed to be unaffected by reduced height.

It was assumed that shorter total height in a southern or southwestern Amazon tree, as compared with a central Amazon tree with the same diameter, translates into a reduced total tree biomass. In order to express the effect of total height as a biomass difference between forest types, tree biomass was estimated based only on dbh (or diameter above buttresses when these structures are present) using the regressions of Higuchi et al. (1998): $\ln(\text{fresh mass}) = -1.754 + 2.665 \times \ln(\text{diameter})$ and $\ln(\text{fresh mass}) = -0.151 + 2.17 \times \ln(\text{diameter})$, respectively for dbh stems 5 – 20 cm and ≥20 cm in diameter. This gives the biomass estimate B_1 for each tree. If B_2 is the total tree biomass in another forest type after correcting only for the height effect, and C_m is a multiplicative correction factor, such that $B_2 = B_1 \times C_m$, then under the assumptions mentioned above, it can be shown that $C_m = 0.66\ (H_{1d}/H_{2d}) + 0.34$; where H_{1d} = expected height in southern or southwestern Amazon forest, at diameter d; and H_{2d} = expected height in central Amazon dense forest, at the same diameter d.

Wood density: effect on biomass

Previous analyses of wood density data of the four forest types (Nogueira et al., 2005, 2007) showed the boles of the trees to be denser in the central Amazon than in the other three forest types ($p = 0.0001$, post-hoc Bonferroni). Wood density is highest in the central Amazon dense forest, lowest in the southwest Amazon bamboo-dominated forest, and has intermediate values in the southwest-Amazon dense forest without bamboo and southern Amazon open forest. As there was no tendency to increase or decrease density as a function of dbh within any of the four forest types (Nogueira et al., 2005, 2007), a single correction factor can be applied to each forest to calculate the effect of wood density on biomass, independent of dbh, either on a tree-by-tree basis or for the total tree biomass per hectare.

The correction factor is the quotient Ws/Wc; where Ws = forest average wood density at breast height in southern or southwestern Amazonia and Wc = dense-forest average wood density at breast height in central Amazonia. The correction factor was multiplied by the dry weight biomass of trees estimated using central Amazon dense forest allometry (Higuchi et al. 1998), in the same way as described above for the height effect.

Results

Height × diameter relationship: trees in southern and southwestern Amazonia tend to be shorter than trees of the same diameter in central Amazonia

The relationships between total tree height and ln(diameter) are shown in three paired regressions (Figure 1). In all three pairs the interaction effect was insignificant ($p = 0.922$, $p = 0.438$ and $p = 0.818$), meaning that the slopes are homogeneous within each pair. Analysis of co-variance of total tree height using forest type as the categorical factor and ln(diameter) as the continuous covariate, showed the intercepts of the three forests in the arc of deforestation to be different from that of the central Amazon forest (ANCOVA $p < 0.001$). Therefore, in all three forest types of the southern and southwest Amazon, trees of any given diameter tend to be shorter than trees of the same diameter in central Amazonia.

[Figure 1 near here]

The correction factor (C_m) outlined in the methods section was applied based on the ratio of the two expected total tree heights at a given diameter. Expected total tree height for any given diameter in each forest type was obtained from the relationship between total height and ln(diameter) in the felled calibration samples. After testing for significant differences, linear regressions between these two variables were developed for each of the four forest types in this study (Table 1).

[Table 1 near here]

The relationship between ln(diameter) and C_m is shown in Figure 2 for each SW Amazon forest and for the southern Amazon forest. Downward corrections of biomass are greatest for trees with smaller diameters and for the bamboo-dominated forest. Considering just the effect of lower tree height for a given diameter, the estimated stand biomass (trees and palms ≥ 5 cm dbh) is lower than in the central Amazon by 11% in SW Amazon open forest with bamboo, 6.2% in SW Amazon dense forest, and 3.6% in the southern Amazon open forests.

[Figure 2 near here]

Generally, the 2/3 scaling exponent previously hypothesized as 'universal' was violated by large trees in the four Amazonian forests studied. When considering trees of all sizes, the scaling exponents found between $\log_{10}$(diameter) and $\log_{10}$(total height) for three of the forest types were significantly lower than the value of 2/3. The exception was SW bamboo-dominated forest, which includes the value 2/3 in the 95% confidence interval (Table 2). For small trees (dbh < 20 cm), the scaling exponent was significantly greater than 2/3 in the SW Amazon dense forest, and not significantly different from 2/3 in the other forest types. These results reinforce the argument that allometric scaling exponents vary in forests with different environmental resources or disturbance regimes.

[Table 2 near here]

Effect on biomass due to wood density differences between trees in southern and southwestern Amazonia and trees in central Amazonia

Based on previously reported mean wood density by forest type (Nogueira et al., 2005, 2007) we estimated the wood density differences expected between central Amazonia and the three other forest types (Table 3). We assumed that average wood density for the entire tree varies in direct proportion to the wood density at breast height. The confidence intervals indicate a 23-33% lowering of biomass for trees (≥5 cm dbh) in the open bamboo-dominated forest, 11-20% lowering of biomass for trees in dense forest without bamboo and 9-15% lowering of biomass for trees in open forest in southern Amazonia. If only the wood density correction were applied, the estimated stand biomass reductions for the three forest types would be 28%, 16% and 12%, respectively.

[Table 3 near here]

Difference in biomass due to both height and wood density

Due to lower height and lighter wood density, trees and palms (≥ 5 cm dbh) in SW Amazon open bamboo-dominated forest, in SW Amazon dense forest and in southern Amazon open forests, biomass stocks were, respectively, 76, 65 and 45 Mg ha^{-1} (dry weight) less than predicted by the uncorrected central Amazon model (Figure 3, Table 4). Considering only the height effect, the estimated biomass reductions for these forests were 21.5, 18.5 and 10.3 Mg ha^{-1}. The effect of lower wood density on biomass estimates is greater than the effect of tree height in all three forest types in the S and SW Amazon regions (Figure 3).

[Figure 3 near here]
[Table 4 near here]

Discussion

These results suggest that biomass per hectare is substantially overestimated by the central Amazon model when applied to the southwestern or southern Amazon without corrections. Although the correction applied makes logical sense, we emphasize that the corrected biomass estimates have not yet been validated by new allometric relationships determined directly by felling and weighing trees in test plots in southern or southwestern Amazonia.

We assessed the difference between measurement heights for dbh (~1.36 m above the ground in central Amazonia and 1.30 m at the other sites). This factor is not believed to have a significant effect on the results. The central Amazon dataset (n=307 trees), where the diameters of all trees were measured (after felling) at 2 or 4 positions along the bole, allowed the taper to be calculated and applied to the 1.30-1.36 cm height interval. Although accuracy decreases for large trees, the diameter at 1.36 m can be calculated to be 0.168% smaller than that at 1.30 m, on average. In addition, we emphasize that the 1.36 m height is an approximate measurement, as mentioned in Nogueira et al. (2005, p. 263), denoted by the symbol: ~1.36 m.

The biomass corrections shown in this paper assume that there is no difference in crown biomass for trees of equal diameter between dense forest in central Amazonia and the three forest types studied in southwestern and southern Amazonia. This may be a conservative assumption. Crown damage was more prevalent in trees infested by abundant climbing bamboos or lianas (Griscom and Ashton, 2006; Alvira et al., 2004) in two widespread open forest types of S and SW Amazonia. On Barro Colorado Island, Panama, Bohlman and O'Brien (2006) found that gap species have smaller crowns than shade species. Gap species are more prevalent in open forests in Amazonia, while shade species are more prevalent in dense forests.

The variation of vegetation structure at the meso scale (i.e., over geographical distances of 1 - 10^3 km) and the concurrent changes of tree form are adaptations to the physical, chemical and ecological conditions of each site (Rozendaal et al., 2006). In this sense, the results in this paper (Figure 1 and Table 2) agree with recent models showing that plant length, diameter, and mass scaling relationships are flexible -- that is, they can vary across species due to species-specific differences in biomass partitioning patterns and ecological responses to different environmental conditions (Muller-Landau et al., 2006; Niklas and Spatz, 2004). However, knowledge is limited of the main factors affecting allometric relationships in tropical forest under different environmental conditions (Malhi et al., 2006).

Recent universal scaling models have linked constraining functional traits related to water and biomass growth with plant size, architecture and allometry (Meinzer, 2003; Niklas and Enquist, 2001; Niklas and Spatz, 2004; West et al., 1999). For example, it is expected that tree height per unit basal area would be reduced with increasing dry-season length (Malhi et al., 2006; Meinzer, 2003; Meinzer et al., 2001). Because of this, trees will be shorter at any given stem diameter in dry seasonal tropical forest. This may contribute to the lower total height of trees in undisturbed forests in southern Amazonia, where the majority of collection sites have a slightly longer dry period (monthly precipitation < 100 mm) than the dense forest in the central Amazon (Brazil, ANA, 2006).

Southern Amazon forests with their longer dry season are also expected to have more abundant lianas (which cause crown damage and probably lower tree height). More lianas are expected because lianas may compete better for access to water throughout the dry season (Mascaro et al., 2004; Restom and Nepstad, 2004) and because light intensity increases below seasonally deciduous tree canopies (Gentry, 1991; Rice et al., 2004). Bamboo-dominated Amazon forests may be associated with both drier climate and substrate. At the peak of the dry season in eastern Acre state, climbing *Guadua* remains evergreen at a time when many tree species drop their leaves. *Guadua* may therefore have a competitive advantage in areas with long dry seasons. Within Amazonia, dense populations of climbing *Guadua* mixed in the forest are largely restricted to a lowland *terra firme* landscape peculiar to the headwaters of the muddy Purus and Juruá Rivers. Here modest tectonic uplift and mechanical erosion have exposed seasonally impermeable 2:1 clays rich in cations (Nelson et al., 2006).

While some previous basin-wide estimates of Amazon carbon stocks have made a correction for wood density, no adjustments have been made for variation in allometric differences such as tree height or crown damage (Baker et al., 2004; Malhi et al., 2006). Available allometric equations for biomass estimates in tropical forest input tree height and wood density as independent variables (Brown et al., 1989; Overman et al., 1994). Although there is no other dataset that has validated the equations developed in central Amazonia, we considered the model by Higuchi et al. (1998) the best equation for central Amazonia (this was also the choice of de Castilho et al., 2006). Another commonly used equation is the model proposed by Chambers et al. (2001) developed from the same dataset but differing mainly due to use of a single cubic fitting, while Higuchi and collaborators proposed two curves (dbh 5-19.9 and ≥20 cm). Our preference for the Higuchi et al. (1998) equations is because Chambers et al. (2001) recognized that their model gave peculiarly low biomass predictions for large trees compared with other models. The cubic curve proposed by Chambers et al. (2001) is based on very few harvested large trees (only 2 trees ≥75 cm dbh). The fit could therefore be spurious. In addition, another dataset collected close to collection sites used both by Higuchi et al. and Chambers showed that there is a slight 'break' at 40 cm dbh in the relation between dbh and bole volume in dense forest in central Amazonia (Nogueira et al, unpublished). Because of this, a better description is obtained if the relationships between dbh and biomass and between dbh and bole volume are represented by two separate equations. Finally, the recent models obtained for biomass of very large trees (e.g., Chave et al., 2005) were not adopted because equations developed locally result in more accurate estimates than equations developed from data originating from several localities, despite their being derived from a large number of trees. A generic equation may not accurately reflect the true biomass of the trees in the specific region (Brown, 2002; Nogueira et al., unpublished).

No allometric models exist that have been validated tree biomass data obtained directly from destructive harvest experiments conducted in southwestern or southern Amazonian forests. Comparing prior biomass estimates from allometric equations with the results of the present study suggests that biomass and carbon stocks have been overestimated for southern Amazonia (e.g., Alves et al., 1997; Feldspausch et al., 2005). Some estimates of tree biomass within the Amazonian 'arc of deforestation' (Cummings et al., 2002) and at open-forest sites where lianas are a dominant life form (Gerwing and Farias, 2000) have employed allometric relationships designed for dense Amazon forest on infertile soils. These may therefore overestimate aboveground tree biomass and greenhouse gas emissions in this part of Amazonia where most deforestation is taking place. Brazil's National Communication under the United Nations Framework Convention on Climate Change (Brazil, MCT, 2004) estimates biomass throughout Brazilian Amazonia based on central Amazonian allometry by Higuchi et al. (1998) applied to tree diameter data from RadamBrasil surveys without correction for either density or tree height.

In spite of recent studies reporting spatial variation in wood density for Amazonia (Baker et al. 2004; Chave et al., 2006; Nogueira et al., 2007), the main environmental factor that explains spatial variation in wood density is still unclear. Environmental and wood density differences between southern, southwestern and central Amazonia have been discussed by recent studies (Baker et al., 2004; Malhi et al., 2006; Nogueira et al., 2007). Lower wood specific gravity as a function of rainfall has been documented more broadly by Wiemann and Williamson (2002). Generally, the main causes suggested to explain the lower stand wood density in southwestern and southern Amazonian forests are related to floristic composition, successional dynamics, edaphic factors and physiological water use principles. The relationship between wood density variation and environmental factors has been particularly difficult to assess due to studies having used different sampling methods (Fearnside, 1997; Nogueira et al., 2005). Our results suggest that the plastic responses of trees to environmental changes are more intense for wood density than for tree height. Assuming that growth rate is inversely proportional to wood density (Enquist et al., 1999; King et al., 2005; Muller-Landau, 2004), the plastic response and hence the resources allocated to tree height will be at least partially dependent on wood density traits. The effect of environmental conditions on tree height will therefore be weaker than their effect on wood density. As the forests in southern Amazonia are more dynamic than those in central Amazonia (Malhi et al., 2006), shorter trees are logical to expect in spite of lower wood density.

Conclusions

In the southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest the trees are shorter than in dense forest in the central Amazon. The height difference was greatest for small trees. Generally the 2/3 scaling exponent suggested as 'universal' was violated by large trees in the four Amazonian forests studied. When the Higuchi et al. (1998) equation (which was developed for use in dense forests) is applied to biomass estimates in open forests of south and southwestern Amazonia, the results have to be corrected for tree height and wood density effects that represent reductions totaling 39% in southwestern Amazon bamboo-dominated open forest, 22% in southwestern Amazon bamboo-free dense forest and 16% in southern Amazonian open forest (respectively, 76, 65 and 45 Mg ha^{-1} lower dry biomass than dense forest in the central Amazon). Considering only the height effect, estimated biomass is lowered by 21.5, 18.5 and 10.3 Mg ha^{-1}, respectively, in the southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest. Revisions are needed in the estimates of biomass that have been made using allometric equations developed in dense forest in the central Amazon. This implies lower emissions of greenhouse gases than previously thought for deforestation in Brazilian Amazonia, which is concentrated in the "arc of deforestation" in non-dense forest types such as the ones we studied.

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Figure legends

Figure 1. Paired regressions of ln(diameter) versus total tree height, compared between central Amazon dense forest (x symbols, dark), two of the southwest Amazon forests and southern Amazon forest (solid circles, gray). A: southwest Amazon open, bamboo-dominated forest, B: southwest Amazon dense forest, C: southern Amazon open forest. D: ln (diameter) versus total height (m) for all four forest types.

Figure 2. Biomass correction factor (Cm) for the effect of lower stem height in the three test forests compared with the central Amazon dense forest. The upper line gives values for southern Amazon open forest the intermediate line for SW Amazon dense forest and the lower line for open, bamboo-dominated forest. D = diameter in centimeters.

Figure 3. Stand biomass for trees + palms ≥5 cm dbh (or above buttresses) in the SW Amazon is adjusted downward by 39% (SW Amazon open, bamboo-dominated forest), 22% (SW Amazon dense forest), and by 16% (southern Amazon open forest) after corrections for lower wood density and shorter tree height as compared with these attributes in central-Amazon dense forest.

Table 1. Parameters of linear regressions for different Amazonian forest types.

Forest type	Parameters* [Total height = $a + b$ ln(diameter)]									
	a *(±SE)*	*a* at CI 95%		***b*** *(±SE)*	*b* at CI 95%		n	dbh range	Adjusted R^2	SEE**
SW Amazon, open bamboo-dominated	-16.223 (1.494)	-19.15	-13.29	11.198 (0.464)	10.29	12.107	91	5 - 85	0.866	3.577
SW Amazon, dense forest	-12.068 (1.883)	-15.81	-8.33	10.672 (0.553)	9.59	11.76	97	5 - 106	0.794	4.185
Central Amazon, dense forest	-11.168 (0.793)	-12.72	-9.61	11.210 (0.254)	10.71	11.708	307	5 - 106	0.864	2.691
Southern Amazon, open forest	-10.678 (0.637)	-11.93	-9.43	10.581 (0.233)	10.12	11.038	264	5 - 124	0.887	2.454

* All parameter values are significant for P-value (p = 0.0001). Three outliers were excluded in the central-Amazon forest, two in the southern-Amazon forest and one in the SW Bamboo forest. For identification of outliers, the studentized residuals (to identify outliers in y space) were plotted against leverage (to identify outliers in x space) and Cook's distance was calculated. Cook's distance measures the influence of each sample observation on the coefficient estimates (Cook and Weisberg, 1982; Wilkinson, 1990).

** Standard Error of the Estimate (SEE) = √Residual Mean-Square

Table 2. Parameters of fitted linear relationships between $\log_{10}$(stem diameter) with $\log_{10}$(tree total height) for different Amazonian forest types, including trees of all sizes, diameter < 20 cm and trees with stem diameter ≥20 cm. Bold values highlight regression slopes.

Forest type		Parameters [$\log_{10}$ (Total height)= a + b $\log_{10}$(diameter)]						
		a (±SE)	CI 95%	*b* (±SE)	CI 95%	n	Adjusted R^2	SEE*
All trees	Dense forest (Central Amazonia)	0.625 (0.018)	0.590 - 0.661	**0.538** (0.013)	0.511 - 0.564	307	0.842	0.061
	Open forest (Southern Amazonia)	0.564 (0.017)	0.530 - 0.597	**0.558** (0.014)	0.530 - 0.586	264	0.851	0.066
	Dense forest (SW Amazonia)	0.494 (0.045)	0.404 - 0.584	**0.576** (0.031)	0.515 - 0.637	97	0.788	0.101
	Open bamboo-dominated forest (SW Amazonia)	0.276 (0.040)	0.197 - 0.354	**0.685** (0.028)	0.628 - 0.741	91	0.867	0.095
Trees < 20 cm in stem diameter								
	Dense forest (Central Amazonia)	0.428 (0.042)	0.346 - 0.510	**0.719** (0.038)	0.645 - 0.794	135	0.729	0.067
	Open forest (Southern Amazonia)	0.448 (0.034)	0.381 - 0.515	**0.673** (0.033)	0.608 - 0.737	199	0.678	0.068
	Dense forest (SW Amazonia)	0.134 (0.124)**	-0.106 - 0.374	**0.919** (0.119)	0.689 - 1.149	30	0.680	0.119
	Open bamboo-dominated forest (SW Amazonia)	0.213 (0.106)***	0.007 - 0.419	**0.737** (0.102)	0.538 - 0.935	41	0.573	0.114
Trees ≥20 cm in stem diameter								
	Dense forest (Central Amazonia)	0.842 (0.035)	0.774 - 0.911	**0.394** (0.023)	0.350 – 0.439	172	0.636	0.046
	Open forest (Southern Amazonia)	0.767 (0.050)	0.671 - 0.863	**0.424** (0.032)	0.363 - 0.485	65	0.741	0.047
	Dense forest (SW Amazonia)	0.817 (0.078)	0.663 - 0.971	**0.379** (0.048)	0.285 - 0.473	67	0.491	0.074
	Open bamboo-dominated forest (SW Amazonia)	0.547 (0.086)	0.378 - 0.716	**0.522** (0.053)	0.419 - 0.625	50	0.672	0.071

* Standard Error of the Estimate (SEE) = $\sqrt{\text{Residual Mean-Square}}$

** Parameter value not significant at the 5% level. Other parameter values (unmarked) are all significant at the 0.1% level.

*** $p = 0.051$.

Table 3. Wood density at breast height (dry weight at 80 °C/green volume with bark) in the four Amazonian forest types.[a]

Forest type	*Sample size (trees ≥ 5 cm dbh)*	*Average basic density at breast height*	*Std deviation*	*Biomass correction factor (± 2 std errors of the ratio of means)*[b]
Central Amazon dense	310	0.712 (0.704)	0.119 (0.117)	---
SW Amazon open bamboo-dominated	92	0.512	0.176	0.718 ± 0.0534
SW Amazon dense	97	0.600	0.160	0.843 ± 0.0482
Southern Amazon open	191	(0.618)	(0.125)	0.877 ± 0.0306

[a] Values in parentheses are dry weight at 103 °C. The biomass correction factor is the ratio between the mean wood density in a given vegetation type and the mean wood density in the central Amazon. For the comparison between southern Amazon open and central Amazon dense forest the wood density values used were for samples dried at 103 ºC at both locations.

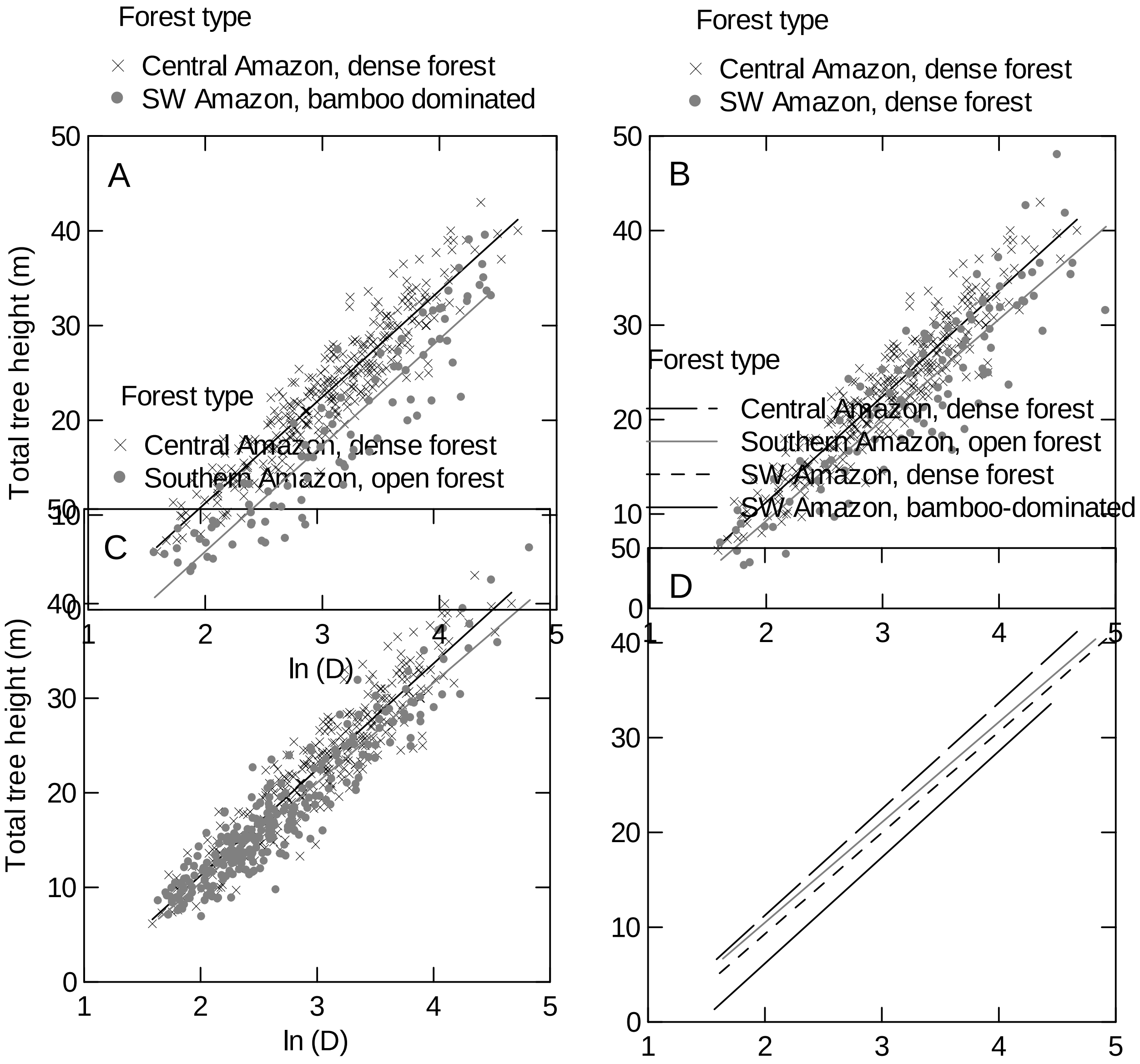
[b] Standard error for a ratio of two estimates (Ott and Longnecker, 2001).

Table 4. Effect of total-height and wood-density corrections on estimated per-hectare biomass[a].

Forest type	*Biomass estimated using central Amazon allometric equation*	*Biomass corrected for height and wood-density difference*	*% Difference*
SW Amazon bamboo-dominated	194 ± 36.8	118 ± 23.4	39%
SW Amazon dense	297 ± 21.6	232 ± 17	22%
Southern Amazon open	285	240	16%

[a] For the two forest types in the southwestern Amazon means ± 1 std. dev. (n=10) are given for trees and palms ≥5 cm dbh (or above buttresses). In the southern Amazon the biomass estimates were obtained from the mean number of trees for each diameter class (5-cm intervals) estimated from 11 ha where trees ≥ 10 cm in diameter were inventoried by Feldpausch et al. (2005) and 30 ha where trees with diameter ≥ 5 cm were inventoried by Pereira et al. (2005).

Figure 1.


Forest type
Central Amazon, dense forest
SW Amazon, bamboo dominated
Forest type
Central Amazon, dense forest
SW Amazon, dense forest
A
B
Total tree height (m)
Forest type
Central Amazon, dense forest
Southern Amazon, open forest
Forest type
Central Amazon, dense forest
Southern Amazon, open forest
SW Amazon, dense forest
SW Amazon, bamboo-dominated
C
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Total tree height (m)
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Figure 2.

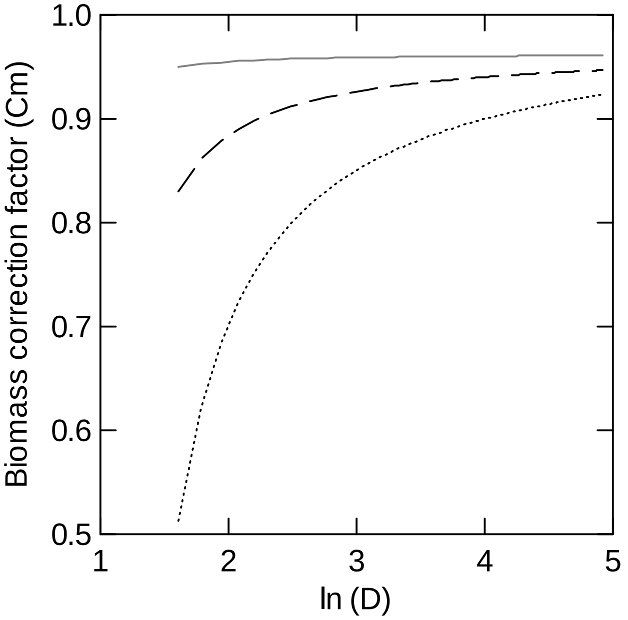
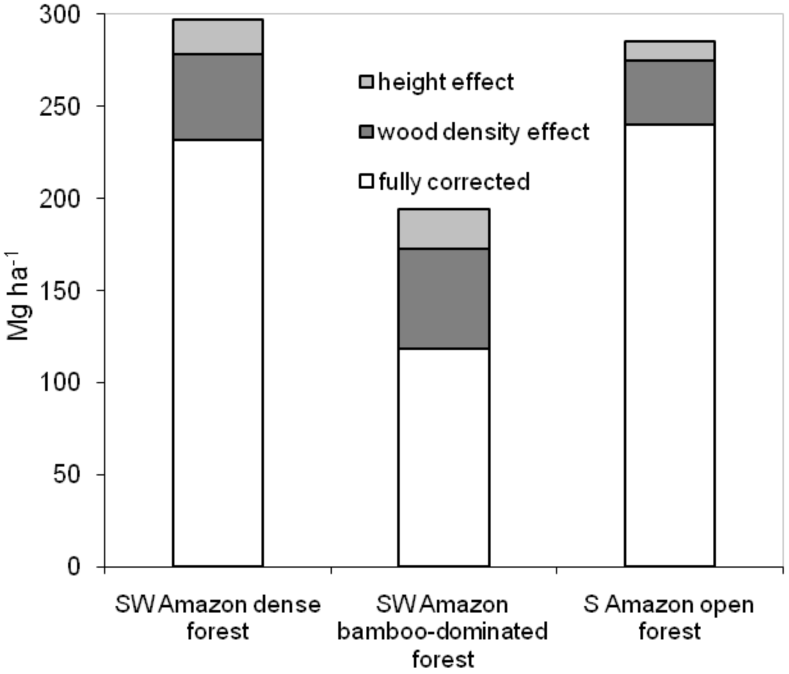


Figure 3.


300
250
200
150
100
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0
Mg ha^{-1}
height effect
wood density effect
fully corrected
SW Amazon dense forest
SW Amazon bamboo-dominated forest
S Amazon open forest