Allometry for Juvenile Trees in an Amazonian Forest after Wind Disturbance

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Abstract

Allometric models to estimate the aboveground mass AGM, belowground mass BGM and total mass TM of juvenile trees (stem diameter at breast height $DBH \le 5$ cm, tree height $H \ge 30$ cm) in open-canopy *terra-firme* forests after wind disturbance were developed in the Amazon. For comparison, the allometric models were also developed for a closed-canopy *terra-firme* forest. After six models had been compared in each forest type, the model with diameter at ground basis DGB and H was selected as the best for estimating AGM and TM, and the model with diameter at ground basis DGB as a single variable was selected as the best for estimating BGM considering the adjusted coefficient of determination and standard deviation of the mean. Models based on the diameter at breast height DBH showed poor correlation with each biomass component compared with those based on DGB for the open-canopy forest. The juvenile trees in the open-canopy forest showed higher AGM and H at a given DGBthan in the closed-canopy forest, while the DGB - BGM relationships did not differ significantly between the open- and closed-canopy forests. It was concluded that the allometric models used to estimate AGM and TM were unique to each forest type. This would be because light-demanding species show higher allocation to AGM than BGM to be advantageous for competition for light by achieving rapid growth in height.

Discipline: Forestry and forest products **Additional key words:** biomass allocation pattern, natural regeneration, wind disturbances

Introduction

A better understanding along the entire life cycle of forest biomass is required to precisely quantify carbon stocks on a regional and national scale. In inventories, it is often assumed that juvenile trees, which are defined as those with a stem diameter at breast height $DBH \le 5$ cm and tree height H > 30 cm in the present study, contribute little to total forest biomass and thus often tend to go unmeasured³. However, their contribution depends on the successional stage of the stand³. In particular, widespread areas of the Amazon are affected by wind disturbance, the impact of which is significant when evaluating forest dynamics and related carbon dynamics in this region⁵. Therefore, there would be a need to account for rapid forest growth during the initial succession stage caused by wind disturbance when evaluating carbon dynamics in Amazonian forests.

To evaluate carbon dynamics, allometric models for estimating biomass in field studies are essential. In the

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Central Amazon, although some allometric models have been reported to estimate biomass in old growth and secondary forests¹⁶, they excluded juvenile trees.

The objectives in the present study were (1) to develop allometric models for estimating biomass for juvenile trees in open-canopy *terra-firme* forest after wind disturbance, and (2) compare the developed allometric models with those for juvenile trees from a closed-canopy *terra-firme* forest to elucidate the generality of the developed models.

Materials and Methods

1. Study sites

The study site is located at an EEST - Experimental Station of Forest Management - (hereinafter referred to as ZF2 site) operated by the National Institute for Amazon Research, Brazil (2°36'S 11°35'W). Some areas dominated by "*terra-firme*" forests on plateaus were significantly disturbed by high-velocity downburst winds in Jan. 2005 (see a previous study¹¹ for details). For comparison, we also sampled in an undisturbed closed-canopy *terra-firme* forest on a plateau (0°7'S 67°3'W) at São Gabriel da Cachoeira in Amazonas state (hereinafter referred to as SG site)¹⁰.

2. Tree individual sampling

During Jul. 2008 and Nov. 2009, 504 juvenile trees (H > 30 cm and *DBH* \leq 5) were sampled from open-canopy terra-firme forest at the ZF2 site, and all samples were collected in pits and the mounds of uprooted trees created by the downburst winds in Jan. 2005. Furthermore, the sample trees were divided into three size categories including small-(n = 289, H < 1 m), middle-(n = 128, 1 m < H < 2 m) and large- (n = 87, 2 m < H) sized juvenile trees. All juvenile trees were measured in terms of TM, with AGM and BGM separately measured for only 215 samples, including mid- and large-sized juvenile trees (n = 128 and 87) respectively. Attempts were made to identify all trees at genus level according to the APG III¹ and 90 genera were recorded (n = 476). The five dominant genera were *Miconia* (n = 50)including Bellucia grossularioides (L.) Triana), Goupia (n = 38 including Goupia glabra Aubl.), Protium (n = 37), Inga (n = 17) and *Pourouma* (n = 17). The species included in the five dominant genera are frequently observed in the early stage of succession, and G. glabra and B. grossularioides were reportedly the main components in the disturbed terra-firme forests¹². Furthermore, for comparison and to test the generality of the developed allometric models, 50 samples were also collected from a closed-canopy terra*firme* forest at the SG site from Sep. to Oct. 2010 (n = 50, $DBH \le 5$ cm). All juvenile trees in the SG site were measured in TM, AGM and BGM. Among the 47 trees, 22 genera were recorded, of which the five dominant genera were Iryanthera (n = 8), Pterocarpus (n = 4), Pouteria (n = 4),



Fig. S1. The relationship between logarithms of diameter at 10% of tree height $D_{0.1}$ [mm] and diameter at ground basis DGB [mm] for juvenile trees in a closed-canopy *terra-firme* (CT) forest (n = 39)

Hevea (n = 4) and Gustavia (n = 4). Those five dominant genera are also frequently observed in undisturbed *terrafirme* forests. For example, *Iryanthera* was reportedly the second most abundant genus in the undisturbed *terra-firme* forest in the SG site¹⁰. Each tree was manually excavated with extreme care to avoid damaging the roots. The diameters at ground basis (*DGB*, mm) and *H* (cm) were measured. However, the *DGB* were not measured for some juvenile trees (n = 11) in the SG site due to accidental loss, and the *DGB* of those juvenile trees were estimated from the diameter at 10% of the tree height (see Fig. S1). The *DBH* (mm) was measured only for large-sized juvenile trees (n = 87 at the ZF2 site). Each sample was oven-dried at 65°C until a constant weight was obtained.

3. Development of allometric models to estimate biomass

To estimate *TM*, *AGM* and *BGM* (kg), the following six models were tested considering previous studies^{7, 10, 14, 16}: model 1: ln (*M*) = *a* + *b* ln (*D*); model 2: ln (*M*) = *a* + *b*ln (*H*); model 3: ln (*M*) = *a* + *b*ln (*D*) + *c*ln (*H*); model 4: *M* = *aD^b*; model 5: *M* = *aH^b*; and model 6: *M* = *aD^bH^c*, where *M* means individual dry mass including *TM*, *AGM* and *BGM*. The *D* (mm) means *DBH* or *DGB*. Here, *a*, *b* and *c* are coefficients. For approximation, ordinary and non-linear least-square methods were applied for Models 1-3 and 4-6, respectively. To determine the best fit model, we evaluated the degree of fit by calculating the adjusted coefficient of determination *R*^{2*} and the standard deviation of the mean $S_{y,x\%}$ (= $\frac{2s}{y\sqrt{n}} \times 100$, where *s*, \overline{y} and *n* are the standard

 Table 1. Coefficients and statistics of six allometric models (1-6) for estimating the biomass component, individual total dry mass TM, aboveground dry mass AGM and belowground dry mass BGM with explanatory variables of diameter at ground basis DGB and tree height H in the ZF2 site

Models for AGM , $n = 215$	а	b	С	CF	$R^{2^{*}}$	S _{y.x%}
1: $\ln (AGM) = a + b \ln(DGB)$	-1.374(±0.199)	2.311(±0.808)		1.123	0.772	4.772
$2: \ln (AGM) = a + b \ln(H)$	-6.490(±0.494)	2.054(±0.094)		1.190	0.486	7.173
3: $\ln (AGM) = a + b \ln(DGB) + c \ln(H)$	-3.842(±0.422)	1.645(±0.127)	0.782(±0.121)	1.102	0.762	4.882
4: $AGM = aDGB^b$	0.161(±0.051)	2.507(±0.098)		1.000	0.781	4.686
5: $AGM = aH^b$	0.001(±0.001)	2.104(±0.174)		1.000	0.49	7.146
$6: AGM = aDGB^bH^c$	0.025(±0.018)	2.218(±0.133)	0.473(±0.159)	1.000	0.792	4.600
Models for BGM , $n = 215$	а	Ь	С	CF	R^{2^*}	$S_{ m y.x\%}$
1: $\ln(BGM) = a + b\ln(DGB)$	-2.643(±0.259)	2.147(±0.105)		1.218	0.564	7.233
$2: \ln (BGM) = a + b \ln(H)$	-6.133(±0.677)	1.667(±0.129)		1.386	0.286	9.260
$3: \ln (BGM) = a + b \ln(DGB) + c \ln(H)$	$-2.703(\pm 0.603)$	2.131(±0.181)	0.019(±0.172)	1.218	0.562	7.253
4: $BGM = aDGB^b$	0.044(±0.021)	2.394(±0.148)		1.000	0.579	7.110
5: $BGM = aH^b$	0.001(±0.001)	1.843(±0.220)		1.000	0.296	9.197
$6: BGM = aDGB^bH^c$	0.063(±0.064)	2.456(±0.222)	0.096(±0.245)	1.000	0.578	7.124
Models for TM , $n = 504$	а	Ь	С	CF	R^{2^*}	$S_{\rm y.x\%}$
1: $\ln(TM) = a + b \ln(DGB)$	-1.819(±0.084)	2.515(±0.041)		1.127	0.813	4.266
$2: \ln (TM) = a + b \ln(H)$	-5.383(±0.179)	1.878(±0.039)		1.196	0.552	6.606
3: $\ln(TM) = a + b \ln(DGB) + c \ln(H)$	-3.531(±0.151)	1.669(±0.074)	0.744(±0.057)	1.094	0.795	4.465
4: $TM = aDGB^b$	0.178(±0.035)	2.528(±0.061)		1.000	0.813	4.262
5: $TM = aH^b$	0.002(±0.001)	2.059(±0.106)		1.000	0.569	6.482
6: $TM = aDGB^bH^c$	$0.044(\pm 0.018)$	2.251(±0.089)	0.392(±0.099)	1.000	0.819	4.198

Each coefficient (a-c) is shown with SE in parentheses. The degree of fitness is indicated by the adjusted coefficient of determination R^{2*} and the standard deviation of the mean $S_{y,x\%}$. The correction factor CF to reduce the bias of log-transformation is shown for Models 1-3.

deviation of the regression, mean of focal variable and the number of samples, respectively). The R^{2*} and $S_{y,x\%}$ for Models 1–3 were calculated based on back-transformed data. To correct the bias introduced by log-transformed data, a correction factor *CF* was calculated as follows¹⁷: $CF = \exp(s^2/2)$. Although the Akaike's Information Criterion AIC was also calculated, the results were not shown since the results of AIC were similar to those based on R^{2*} and $S_{y,x\%}$. All regression analyses were conducted using statistical software R ver. 2.14.0.

4. Comparisons of allometric models between openand closed-canopy forests

To confirm the generality of the allometric models developed for juvenile trees in the open-canopy *terra-firme* forest (OT) at the ZF2 site, the models were compared with those for juvenile trees in the closed-canopy *terra-firme* forest (CT) at the SG site (n = 50). A comparison was performed for the relationships of *AGM*, *BGM* and *TM* to *DGB* according to the analysis of covariance (ANCOVA). The ANCOVA was performed after log-transformation of the variables, i.e. Model 1 compared two different forest types for each biomass component. Similarly, the *DGB* – *H* and *AGM* – *BGM* relationships were also compared with those

from the SG site.

Results and Discussion

Six models were evaluated for each biomass component in the open-canopy terra-firme forest (OT) at the ZF2 site (Table 1) and the closed-canopy terra-firme forest (CT) in the SG site (Table 2). For TM and AGM, Models 3 and 6 with *DGB* achieved the highest R^{2*} and the lowest $S_{\nu,x\%}$ in each site. For *BGM*, Model 4 achieved the highest R^{2*} and lowest $S_{y,x\%}$ in each site. Interestingly, H did not improve the fitting for estimating BGM, i.e. Model 6 including H showed lower R^{2*} and higher $S_{y,x\%}$ than Model 4. Model 4 could be applied without H measurement and thus showed superior working efficiency to the other models requiring H measurement. Although H did not improve the fitting for each biomass component in the OT forest, Himproved the fitting for AGM and TM in the CT forest. In terms of general versatility and accuracy of the model, it was concluded that the best models were 6 for estimating AGM and TM, and 4 for estimating BGM in the present study sites.

Using 87 samples (H > 2 m) in the OT forest, allometric models with *DBH* were also compared to those

 Table 2. Coefficients and statistics of six allometric models (1-6) for estimating the biomass component, individual total dry mass TM, aboveground dry mass AGM and belowground dry mass BGM with explanatory variables of diameter at ground basis DGB and tree height H in the SG site

Models for AGM , $n = 50$	а	Ь	С	CF	R^{2^*}	$S_{\rm y.x\%}$
1: $\ln (AGM) = a + b \ln(DGB)$	-10.648(±0.183)	3.028(±0.067)		1.103	0.854	11.59
$2: \ln (AGM) = a + b \ln(H)$	-3.912(±0.088)	2.584(±0.076)		1.185	0.872	10.83
$3: \ln (AGM) = a + b \ln(DGB) + c \ln(H)$	-8.265(±0.497)	1.950(±0.221)	0.958(±0.190)	1.067	0.930	8.04
4: $AGM = aDGB^b$	$0.0003(\pm 0.0004)$	2.383(±0.307)		1.000	0.901	9.52
5: $AGM = aH^b$	0.023(±0.012)	2.717(±0.249)		1.000	0.932	7.90
$6: AGM = aDGB^bH^c$	0.003(±0.003)	0.931(±0.323)	1.881(±0.316)	1.000	0.943	7.25
Models for <i>BGM</i> , $n = 50$	а	b	С	CF	R^{2^*}	$S_{ m y.x\%}$
1: $\ln(BGM) = a + b\ln(DGB)$	-10.799(±0.285)	2.616(±0.104)		1.269	0.316	23.81
$2: \ln (BGM) = a + b \ln(H)$	-4.981(±0.112)	2.238(±0.097)		1.320	0.656	16.89
$3: \ln (BGM) = a + b \ln(DGB) + c \ln(H)$	-8.531(±0.895)	1.591(±0.399)	0.911(±0.343)	1.236	0.522	19.91
4: $BGM = aDGB^b$	$0.002(\pm 0.002)$	1.531(±0.274)		1.000	0.714	15.39
5: $BGM = aH^b$	0.023(±0.016)	1.759(±0.339)		1.000	0.677	16.36
$6: BGM = aDGB^bH^c$	0.001(±0.001)	1.853(±0.595)	-0.360(±0.547)	1.000	0.710	15.51
Models for TM , $n = 50$	а	Ь	С	CF	R^{2^*}	$S_{\rm y.x\%}$
1: $\ln(TM) = a + b \ln(DGB)$	-10.136(±0.191)	2.944(±0.070)		1.113	0.826	12.34
$2: \ln (TM) = a + b \ln(H)$	-3.588(±0.090)	2.511(±0.077)		1.193	0.890	9.819
3: $\ln(TM) = a + b \ln(DGB) + c \ln(H)$	-7.851(±0.540)	1.910(±0.241)	0.918(±0.207)	1.080	0.922	8.261
4: $TM = aDGB^b$	0.001(±0.001)	2.204(±0.264)		1.000	0.905	9.119
5: $TM = aH^b$	0.035(±0.018)	2.577(±0.237)		1.000	0.928	7.919
6: $TM = aDGB^bH^c$	0.006(±0.006)	0.883(±0.316)	1.705(±0.317)	1.000	0.938	7.348

Each coefficient (a-c) is shown with SE in parentheses. The degree of fitness is indicated by the adjusted coefficient of determination R^{2^*} and the standard deviation of the mean $S_{y,x\%}$. The correction factor CF to reduce the bias of log-transformation is shown for Models 1-3.

with *DGB* (Table 3). Overall, models with *DBH* showed poor fitting results compared to those with *DGB* in each case, i.e. *DBH*-based models showed lower R^{2*} and higher $S_{y,x\%}$ than corresponding models based on *DGB*. Although *DGB* showed higher accuracy for estimating dry mass, the use of *DGB* would be inconvenient for relatively large trees. This is because stems tend to be shaped irregularly near the ground, which results in inaccuracy when estimating the dry mass of large trees, especially those with buttresses. Therefore, the use of *DGB* can only be recommended for juvenile trees.

To confirm the generality of developed models for open-canopy *terra-firme* forest, the models were compared with those from the closed-canopy *terra-firme* forest at the CT forest. As depicted in Fig. 1, the *DGB* - *AGM* relationships differed significantly between them (slope, $F_{1,259} =$ 44.82, $p = 1.32 \times 10^{-10} < 0.001$). Within the observed range of *DGB*, the *AGM* for a given *DGB* tended to be higher in the open-canopy forest than in the closed-canopy forest. Conversely, the *DGB* - *BGM* relationship did not differ significantly between them (slope, $F_{1,259} = 10.56$, p = 0.0013 >0.001; intercept $F_{1,260} = 0.578$, p = 0.448 > 0.05). Consequently, the *DGB* - *TM* relationship showed a significant difference (slope, $F_{1,551} = 6.01$, $p = 6.32 \times 10^{-09} <$

0.001).

The AGM and TM at a given DGB were higher in the open-canopy forest than in the closed-canopy forest, which is partly attributable to the differences in H, since the H at a given DGB was significantly higher in the open- rather than closed-canopy forest (Fig. 2a), i.e. the DGB - H relationship differed significantly in the intercept with a common slope (slope, $F_{1,550} = 0.042$, p = 0.839 > 0.05; intercept $F_{1,551} =$ 18.02, $p = 2.57 \times 10^{-5} < 0.001$). Light-demanding species tend to be taller than shade-tolerant species for a given diameter^{6, 8, 13} since the former grow rapidly to reach the canopy and gain a competitive advantage in the struggle for light. It has been reported that the differences in size between functional types were only present in the early stages of plant development². The present study also confirmed that the difference in the DGB - AGM relationships became unclear with increasing size (Fig. 1a).

In addition, the AGM - BGM relationship also showed significant difference in the intercept with a common slope (Fig. 2b) (slope, $F_{1, 259} = 0.001$, p = 0.977 > 0.05; intercept $F_{1, 260} = 26.163$, $p = 6.097 \times 10^{-7} < 0.001$), and the *BGM* for a given *AGM* was lower in the open- rather than closed-canopy forest. Similarly, light-demanding species reportedly show a lower root / shoot ratio than shade-tolerant spe-

Models for AGM with DBH , $n = 87$	а	b	С	CF	$R^{2^{*}}$	$S_{\rm y.x\%}$
1: $\ln (AGM) = a + b \ln (DBH)$	1.144(±0.351)	1.618(±0.141)		1.138	0.531	7.308
3: $\ln (AGM) = a + b \ln (DBH) + c \ln(H)$	0.235(±1.708)	1.315(±0.231)	0.211 (±0.375)	1.140	0.528	7.332
4: $AGM = aDBH^b$	1.660(±0.967)	1.901(±0.195)		1.000	0.548	7.173
$6: AGM = aDBH^bH^c$	0.267(±0.494)	1.774(±0.236)	0.374 (±0.360)	1.000	0.549	7.166
Models for <i>BGM</i> with <i>DBH</i> , $n = 87$	а	b	С	CF	$R^{2^{*}}$	S _{y.x%}
1: $\ln(BGM) = a + b \ln(DBH)$	-0.627 (±0.549)	1.596 (±0.218)		1.368	0.327	10.317
3: $\ln(BGM) = a + b \ln(DBH) + c \ln(H)$	0.212 (±2.643)	1.688 (±0.358)	-0.189(±0.580)	1.367	0.321	10.567
4: $BGM = aDBH^b$	0.349 (±0.298)	1.859(±0.287)		1.000	0.334	10.458
$6: BGM = aDBH^bH^c$	0.608 (±1.655)	1.896 (±0.347)	-0.113 (±0.539)	1.000	0.327	10.518
Models for TM with DBH , $n = 87$	а	b	С	CF	R^{2^*}	$S_{\rm y.x\%}$
1: $\ln(TM) = a + b \ln(DBH)$	1.330(±0.365)	1.611(±0.145)		1.148	0.515	7.480
3: $\ln(TM) = a + b \ln(DBH) + c \ln(H)$	0.720(±1.761)	1.545(±0.238)	0.137(±0.386)	1.149	0.51	7.515
4: $TM = aDBH^b$	2.005(±1.198)	1.894(±0.200)		1.000	0.531	7.353
6: $TM = aDBH^bH^c$	0.466(±0.887)	1.794(±0.242)	0.299(±0.371)	1.000	0.529	7.367
Models for AGM with DGB , $n = 87$	а	Ь	С	CF	$R^{2^{*}}$	$S_{\mathrm{y.x\%}}$
1: $\ln (AGM) = a + b \ln(DGB)$	-0.760(±0.429)	2.125(±0.153)		1.106	0.678	6.046
3: $\ln (AGM) = a + b \ln (DGB) + c \ln(H)$	-2.903(±1.212)	1.870(±0.202)	0.504(±0.267)	1.103	0.683	6.005
4: $AGM = aDGB^b$	0.180(±0.105)	2.474(±0.181)		1	0.698	5.860
$6: AGM = aDGB^bH^c$	0.017(±0.024)	2.249(±0.212)	0.526(±0.289)	1	0.706	5.781
Models for BGM with DGB , $n = 87$	а	b	С	CF	R^{2^*}	$S_{ m y.x\%}$
1: $\ln(BGM) = a + b \ln(DGB)$	-3.360(±0.621)	2.402(±0.221)		1.239	0.477	9.263
3: $\ln(BGM) = a + b \ln(DGB) + c \ln(H)$	-2.249(±1.788)	2.535(±0.298)	-0.261(±0.339)	1.238	0.472	9.312
4: $BGM = aDGB^b$	0.042(±0.379)	2.411(±0.281)		1.000	0.478	9.263
$6: BGM = aDGB^bH^c$	0.092(±0.206)	2.487(±0.359)	-0.177(±0.468)	1.000	0.473	9.310
Models for TM with DGB , $n = 87$	а	b	С	CF	R^{2^*}	$S_{\rm y.x\%}$
1: $\ln(TM) = a + b \ln(DGB)$	-0.686(±0.426)	2.159(±0.151)		1.105	0.673	6.134
3: $\ln(TM) = a + b \ln(DGB) + c \ln(H)$	-2.317(±0.215)	1.965(±0.203)	0.383(±0.267)	1.104	0.675	6.124
4: $TM = aDGB^b$	0.221(±0.132)	2.464(±0.184)		1.000	0.688	5.994
6: $TM = aDGB^bH^c$	0.033(±0.049)	2.284(±0.221)	0.421(±0.298)	1.000	0.692	5.960

Table 3. Comparisons of four allometric models (1, 3, 4 and 6) based on DGB and DBH for estimating the biomass
component, including individual total dry mass TM, aboveground dry mass AGM and belowground dry mass
BGM in the ZF2 site

Each coefficient (a-c) is shown with 95% confidence intervals in parentheses. The degree of fitness is indicated by the adjusted coefficient of determination R^{2*} and the standard deviation of the mean $S_{y,x\%}$. The correction factor CF to reduce the bias of log-transformation is shown for Models 1 and 3.

cies^{4,9,15}. The low root / shoot ratio in the light-demanding species may also be partly attributable to the rapid height growth of light-demanding species to gain a competitive advantage in the struggle with neighboring trees for light^{6,8,13}.

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Fig. 1. The relationships between logarithms of diameter at ground basis *DGB* [mm] and biomass components including (a) aboveground dry mass *AGM* [g], (b) belowground dry mass *BGM* [g] and (c) total dry mass *TM* [g] for two different forest types

The circles and squares indicate data from open- and closed-canopy *terra-firme* forests (OT and CT) respectively. The solid and dashed lines in figures (a) and (c) mean regression lines for OT and CT, respectively. The solid line in Figure (b) means the common regression line for OT and CT.



Fig. 2. (a) The relationships between logarithms of diameter at ground basis *DGB* [mm] and tree height *H* [cm], and (b) The relationships between logarithms of individual aboveground and belowground dry mass *AGM* and *BGM* [g] respectively for two study sites

The circles and squares indicate data from open-canopy *terra-firme* and closed-canopy *terra-firme* forests (OT and CT). The solid and dashed lines mean regression lines for OT and CT, respectively.

Allometry for Juvenile Trees after Wind Disturbance in the Amazon

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