THE BIOMASS OF BAMBOO (GUADUA WEBERBAUERI PILGER) IN OPEN FOREST OF THE SOUTHWESTERN AMAZON

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Resumo. Análise de regressão foi usada para construir equações para o cálculo da biomassa de uma espécie de bambu (Guadua weberbaueri Pilger) dominante em florestas do oeste da Amazônia. As equações foram usadas em combinação com uma equação para estimativas de biomassa de árvores em uma área de floresta ombrófila aberta dominada por bambu próximo a Rio Branco, Acre, Brasil. Os resultados indicaram o uso do diâmetro à altura do peito e altura para as estimativas de biomassa, e que o bambu, mesmo não retendo uma biomassa muito grande, está entre as espécies menos densas com mais biomassa, e possivelmente tem um efeito de reduzir o acúmulo de biomassa por parte das árvores, reduzindo a biomassa aérea total em grupos com densidades altas de colmos. Sua habilidade de colonizar claras e áreas perturbadas e reprodução e mortalidade em massa aumentam a sua importância no funcionamento do ecossistema.

Abstract. Regression analysis was used to create equations for biomass calculations of a tropical forest understory dominant bamboo, Guadua weberbaueri Pilger. The equations were used in combination with a general equation for trees in mature forest to calculate the biomass of bamboo and trees in a 3,000 m² sample area in a bamboo-dominated open rain forest near Rio Branco, Acre, Brazil. The results suggest that it is possible to use diameter at breast height (DBH) and height to estimate bamboo biomass, and although bamboo biomass is not a high proportion of total biomass, it is among the most biomass-retaining species, and possibly has the effect of arresting biomass accumulation by trees, reducing total aboveground biomass in stands with high bamboo densities. Its ability to colonize gaps and disturbed areas and its mass reproduction and mortality enhance its importance in ecosystem functioning. Accepted 25 May 2000.

Key words: Tropical forest, biomass, Neotropical bamboo, Guadua weberbaueri.

INTRODUCTION

Bamboo forest, a facies of the open rain forest (Velasco et al. 1991), is characterized by the dominance of arborescent bamboos of the Guadua genus and covers about 50% of Acre state in the southwestern Brazilian Amazon (Nelson 1994a).

Despite some remote sensing data (Nelson 1994b), much remains unknown about this kind of forest. Among the most important aspects not yet studied are the resource partitioning relationships between the dominant plant species, including the bamboos. The biomass of tree species in tropical forests has been studied using carbon-stock, land-use and global change approaches (e.g., Bekkering 1992, Brown et al. 1992, Sombroek 1992). In these studies, biomass calculations were done using equations obtained by destructive methods or by wood-volume and density estimates. These equations may be applied to entire second-growth communities (Williams-Linera 1983, Brown & Lugo 1990), or mature ones (Brown & Lugo 1992, Sombroek 1992), or combined in species-specific equations (Uhl et al. 1988).

The arborescent habits and competitive ability of forest bamboos, as well their fast growth (9 to 30 cm/day for culms; Shanmughavel & Francis 1996, Pearson et al. 1994) are important in understanding their role in forest structure. The long time period to sexual reproduction (up to 120 years; Janzen 1976) and subsequent death make the influence of bamboo on forest dynamics even more important.

The equations used for biomass calculations in secondary or mature forests, based on arboreal dicots, are not adequate for arborescent bamboo, with its particular growth form (hollow culms, secondary growth absent). Stem abundance could vary in the physiognomic units of southwestern Amazon bamboo forests, only in extreme cases forming a near-pure stand locally called Tabocal, which may cover large areas.

Previous work on bamboo biomass has concentrated on Asia (e.g., Isagi et al. 1993, 1997; Shanmughavel & Francis 1996; Tripathi & Singh 1996)
with a few papers dealing with Neotropical Chusquea bamboos, such as Veblen et al. (1980), Pearson et al. (1994) and Tol & Cleef (1994).

Most of the sympodial bamboos can reach very high densities (Isagi et al. 1993), and have clustered distributions. The bamboos of the monopodial genus Phyllostachys tend to have spaced culms forming large stands, instead of clumps, and sometimes reach a very high biomass (Isagi et al. 1997).

In the Neotropical genus Guadua, the rhizomes run below ground for tens of meters, putting out new culms, very densely in the clearings (both treefall gaps and small slash-and-burn sites) and more spaced in the shade, resulting in an "ever-expanding" pattern. The older colonized areas are denser while the newer have few and spaced young culms even in the shade (Silveira unpubl. data). After reaching 10–15 m in height, the culms use their spines to climb the canopy trees, changing the forest structure. In the larger treefall gaps and abandoned slash-and-burn agricultural sites, the density of culms is the highest possible, sometimes forming layers of fallen culms.

With the aim of providing a tool for estimating the contribution of bamboo to the aboveground biomass of bamboo forests we calculated regressions of morphometry in dry mass for Guadua weberbaueri Pilger, a climbing and spiny bamboo very abundant in the understory of bamboo-dominated forests in the Acre river valley, and tested them in samples of bamboo and tree species.

METHODS

Study area. The Catuaba Farm, belonging to Acre Federal University, is in southeast Acre state (9°57'S, 67°52'W), 27 km from Rio Branco city, and has a total area of 680 ha. The land cover includes pasture, second growth forest and mature forest with (mostly) and without bamboo. The vegetation can be classified as open rain forest (Velasco et al. 1991), where the canopy is not continuous and the dense understory has life forms such as palms and bamboos.

In 1983 the populations of G. weberbaueri of the Catuaba Farm died off after flowering/fruiting, with only some patches remaining alive (in 1985) ranging from 1 to 4 ha. Since that time the remaining patches have increased in size, beginning to coalesce in 1996.

Sampling data for regressions. In one patch we selected 20 culms (healthy plants and without breaks) which after measuring DBH (diameter at breast height) and estimating total height, were cut at ground level then classified in three groups: (1) Shoots (the sheaths still remain, there are no thorns, branches or leaves), (2) Young culms (culms with some branching, with few leaves and thorns), and (3) Adults (culms full of branches, leaves and thorns). The shoots and young culms have soft, non-lignified stem walls and erect ends, while in adults the walls are hard and the ends are bent.

After cutting, the total length was measured to verify the accuracy of height estimation, and for each sample the stem, branches and leaves were separated. A field weighing was done with dynamometers and subsamples of each portion were again weighed, and dried at 70° C until mass was constant (3–5 days). All work with each culm was done at one time (around 30 minutes), and all the culms were sampled in one week in the late rainy season (May).

A fresh/dry mass ratio for each portion was also calculated. The values of fresh/dry mass ratios was subjected to an ANOVA (analysis of variance) to show differences in the water content between the three groups (shoots, young culms and adults).

Regression analysis was done using the data from the three groups together and separately. We calculated equations using total height, DBH and DBH plus total height as independent variables.

Using the equations. As a trial, the equations were used with data from an inventory (3000 m²) of a bamboo forest in the same area (Catuaba Farm; Silveira et al., in prep.), in combination with a general equation for tree species in a similar mature forest as presented by Brown et al. (1995). The inventory was divided into three parallel lines (transects) measuring 5 by 200 m, which were 10 to 20 m distant from each other. All trees and bamboo with 2.5 cm or more DBH were included.

RESULTS

Group or growth stage differentiation. The analysis of variance (ANOVA) of fresh/dry mass ratios showed significant differences only between adult culms and shoots/young culms combined (P < 0.001).

The average fresh/dry mass ratio for shoots + young culms (0.285 ± 0.031) was lower than that for adults (0.386 ± 0.066). Thus the regressions calculated for the three groups combined showed lower r² than for the two groups adults and shoots + young culms (Table 1). This led us to use separate regressions for the two groups.
TABLE 1. Summary of regressions calculated for Guadua weberbaueri, with $P < 0.01$ (*) and $P < 0.05$ (#).

<table>
<thead>
<tr>
<th>Groups</th>
<th>Allometry</th>
<th>Transformation</th>
<th>Equation No</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A+Y+S</td>
<td>Height+DBH</td>
<td>Linear</td>
<td>–</td>
<td>0.445</td>
</tr>
<tr>
<td>A+Y+S</td>
<td>Height</td>
<td>Potential</td>
<td>–</td>
<td>0.4093</td>
</tr>
<tr>
<td>A+Y+S</td>
<td>DBH</td>
<td>Potential</td>
<td>–</td>
<td>0.3793</td>
</tr>
<tr>
<td>A</td>
<td>Height+DBH</td>
<td>Linear</td>
<td>1</td>
<td>0.748#</td>
</tr>
<tr>
<td>A</td>
<td>Height</td>
<td>Potential</td>
<td>–</td>
<td>0.3365</td>
</tr>
<tr>
<td>A</td>
<td>DBH</td>
<td>Polynomial (3rd)</td>
<td>2</td>
<td>0.8149*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>2</td>
<td>0.7261#</td>
</tr>
<tr>
<td>Y+S</td>
<td>Height+DBH</td>
<td>Linear</td>
<td>4</td>
<td>0.7568#</td>
</tr>
<tr>
<td>Y+S</td>
<td>Height</td>
<td>Potential</td>
<td>–</td>
<td>0.4764</td>
</tr>
<tr>
<td>Y+S</td>
<td>DBH</td>
<td>Exponential</td>
<td>5</td>
<td>0.6787#</td>
</tr>
</tbody>
</table>

$A =$ adult culms, $Y =$ young culms, $S =$ shoots. Grouped according to age.

Using different variables. The regressions using both DBH and estimated height as independent factors resulted in better correlation coefficients and smaller standard errors than using only DBH, which in turn was better than using only height (Figs. 1 and 2).

In very dense stands the bamboos may form a layer, making the estimation of height very difficult. Equations using only estimated height have weak correlations due to this problem. The correlation coefficient between estimated height and total length was significant ($r^2 = 0.48$, $P > 0.05$, $n = 20$) but still weak.

Equations:

1. $Y = 0.2254X_1 + 4.969X_2 - 20.171$ (Equation A)
2. $Y = 2.928X_1^3 - 37.554X_1^2 + 161.23X_1 - 226.54$ (Eq. B)
3. $Y = 5.4922X_1 - 19.516$ (Eq. C)
4. $Y = 0.172X_1 + 1.18X_2 - 4.478$ (Eq. D)
5. $Y = 0.2756 e^{0.512X_1}$ (Eq. E)

($X_1 =$ estimated height, $X_2 =$ DBH)

Those equations which have an acceptable correlation coefficient can only be used within the DBH and total height interval sampled. The ranges from 3.5 to 6.2 cm of DBH and 8 to 20 m in height include 96.5% (DBH) and 91.5% (height) of the 426 culms in our 3000 m² sample area.

Trial results. The results in Table 2 show that only 4.2% of aboveground live biomass is bamboo (10.2 t.ha⁻¹). However, we find G. weberbaueri in a surprising 7th position in a biomass ranking of species, above many canopy and understory tree species.

In a pure bamboo stand in Japan, Isagi et al. (1993) report an average of 113 t.ha⁻¹, with average density of 1.16 culms/m², against the 0.142 culms/m² of this study. In the same paper, the authors present data from literature ranging from 30.1 t.ha⁻¹ (at 3.52 culms/m²) to 161.7 t.ha⁻¹ (at 18.7 culms/m²) for different species in pure stands.

In Fig. 3, data on bamboo densities and tree biomass are compared, excluding from line 3 a very large (146 cm DBH, 35 m height) individual of *Pterocarpus* sp. which accounted for 50% of the biomass (22 tons) of that sample. With this procedure, the evidence for arrested biomass accumulation by canopy and understory trees as a function of bamboo dominance is highlighted. The individual removed from line 3 was the only emergent sampled; another of the biggest trees reached only 4.6 ton. Santos (in prep.)

![Figure 1](image-url)  
**FIG. 1.** Relationship between dry mass and estimated height in adults and shoots+young bamboo culms.
FIG. 2. Relationship between dry mass and DBH in adults and shoots plus young bamboo culms.

refers to only 94 t/ha of total biomass, with 0.254 bamboo stems/m², in a forest of the same region. In our study, with a mean of 0.142 bamboo stems/m², the total biomass reached 240.9 t/ha⁻¹.

In the data in Fig. 3, we have only 17% of variation in bamboo density and 66% in tree biomass. Even the increase in bamboo biomass (44%) in absolute terms cannot compensate for the loss in tree biomass (plus 0.64 t of bamboo, minus 13 t of trees).

DISCUSSION

Research on biomass and carbon stock of the bamboo forest needs to consider the contribution of this dominant life form. In spite of its growth form it was possible to use linear regression to achieve this.

The differences found in water content and presence of branches and leaves show that there should be separate estimates for shoots, young culms and adults. In the field, classification into these categories is easy and fast, because the development of the stems is accompanied by strong visual differences like lateral branching, thorns, and emergence of leaves.

The high growth rate of shoots and young culms (up to 15cm/day, Silveira 1999) resulted in younger stems of the same height, with higher water content and less leaves than adults, or no leaves at all. Fast growing is common for both Neotropical (Pearnson et al. 1994) and Old World bamboos (Shanmugavel & Francis 1996).

The differences in water content supported the use of separate regressions for two groups (adults and shoots + young culms). Studying Phyllostachys bam-

FIG. 3. Comparison of bamboo culm density and tree biomass for each sample line (1000 m²).

### TABLE 2. Biomass estimates for 3000 m² sample.

<table>
<thead>
<tr>
<th>Species/groups</th>
<th># stems</th>
<th>kg/3000m²</th>
<th>ton/ha</th>
<th>% total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pterocarpus sp.</td>
<td>2</td>
<td>22451.6</td>
<td>74.8</td>
<td>31.1</td>
</tr>
<tr>
<td>Licaria sp.</td>
<td>2</td>
<td>5296.6</td>
<td>17.7</td>
<td>7.3</td>
</tr>
<tr>
<td>Sterculia sp.</td>
<td>2</td>
<td>3988.4</td>
<td>13.3</td>
<td>5.5</td>
</tr>
<tr>
<td>Castilia ulei</td>
<td>4</td>
<td>3953.7</td>
<td>13.2</td>
<td>5.5</td>
</tr>
<tr>
<td>Tachigali sp.</td>
<td>6</td>
<td>3806.6</td>
<td>12.7</td>
<td>5.3</td>
</tr>
<tr>
<td>Inga alba</td>
<td>3</td>
<td>3420.9</td>
<td>11.4</td>
<td>4.7</td>
</tr>
<tr>
<td>Eschweidera sp.</td>
<td>4</td>
<td>2786.0</td>
<td>9.3</td>
<td>3.9</td>
</tr>
<tr>
<td>Byronima sp.</td>
<td>1</td>
<td>2200.7</td>
<td>7.3</td>
<td>3.0</td>
</tr>
<tr>
<td>Himenolobium sp.</td>
<td>2</td>
<td>1830.6</td>
<td>6.1</td>
<td>2.5</td>
</tr>
<tr>
<td>Viola diversa</td>
<td>6</td>
<td>1727.3</td>
<td>5.8</td>
<td>2.4</td>
</tr>
<tr>
<td>Others</td>
<td>449</td>
<td>17744.0</td>
<td>59.1</td>
<td>24.6</td>
</tr>
<tr>
<td>Total of arboresic dicots + palms</td>
<td>531</td>
<td>69206.4</td>
<td>230.7</td>
<td>95.8</td>
</tr>
<tr>
<td>Bamboo</td>
<td>426</td>
<td>3059.7</td>
<td>10.2</td>
<td>4.2</td>
</tr>
<tr>
<td>Total</td>
<td>–</td>
<td>72266.1</td>
<td>240.9</td>
<td>100</td>
</tr>
</tbody>
</table>
busoides in Japan, Isagi et al. (1993) employed a similar grouping.

We recommend the use of equations 1 and 4 (Table 1) if good height estimates are available. If the samples include only DBH measurement, equations 2, 3 and 5 are better. No equations match data with height only.

The importance of bamboo to the forest above-ground biomass may be considered either directly (by dividing biomass between species) or by the possible effect on the biomass accumulation, recruitment and mortality of another species.

We suggest that samples in places with higher bamboo densities will show lowest total above-ground biomass, as a consequence of changes in forest structure. These changes may be related both to regeneration problems and morality of adult trees caused by bamboo.

A single individual of a large emergent species, like Pterocarpus sp., is able to account for up to twice the bamboo biomass in one hectare. For a carbon-stock approach, bamboo may contribute only a small proportion of the total biomass, but in terms of partition of resources it plays an important role because of its dominance in the understory and possible reducing effect on the total biomass, as suggested in Fig. 3.

Thus, bamboo can have a strong influence over the capacity of forests to sequester carbon, causing losses in total forest carbon-stock in the course of their life cycle in a way that no natural phenomena like treefall gaps and hurricanes can do. The 94 t/ha of total above-ground biomass reported by Santos (in prep.), with a still higher bamboo density, help to corroborate our statements.

Because of the heavy layering of the culms when no supporting trees are available, a pure or near pure stand of Guadua will never reach the biomass reported by Isagi et al. (1997) for Phyllostachys pubescens stand (149 t/ha), so no compensation for the losses in tree biomass by bamboo biomass increase can be expected.

The events of mass flowering followed by population-wide mortality are also strong grounds for concern about bamboo biomass. No tree species can put tens of tons of dead material into the soil at one time. Besides the rapid changes in forest structure, this may lead to changes in nutrient cycling, soil microbiota dynamics (G. Andrade, pers. comm.), and consequently in ecosystem functioning.

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