

The text that follows is a PREPRINT.

Please cite as:

Nogueira, E.M., B.W. Nelson and P.M. Fearnside. 2006. Volume and biomass of trees in central Amazonia: Influence of irregularly shaped and hollow trunks. *Forest Ecology and Management* 227(1-2): 14-21.

DOI 10.1016/j.foreco.2006.02.004

ISSN: 0378-1127

Copyright: Elsevier

The original publication is available at: <http://www.elsevier.com.nl> [<publisher link>](#)

1
2
3 **Volume and biomass of trees in central Amazonia:**
4 **Influence of irregularly shaped and hollow trunks**
5

6 Euler Melo Nogueira^a; Bruce Walker Nelson^b, Philip M. Fearnside^{b*}

7
8 ^aProgram in Tropical Forest Science, National Institute for Research in the Amazon–INPA,
9 C.P. 478, 69.011-970 Manaus, Amazonas, Brazil.

10
11 ^bDepartment of Ecology, National Institute for Research in the Amazon–INPA, C.P. 478,
12 69.011-970 Manaus, Amazonas, Brazil.

13
14 * Corresponding author. e-mail: pmfearn@inpa.gov.br
15
16
17

18 Revised 5 Feb. 2006
19
20

21 Main text 4612 words; total 5989 words.

Abstract

Conventional measurements of diameter, basal area and volume of the bole assume that any cross section of the bole is circular and that the bole is a solid of revolution. These assumptions lead to error when the bole is irregularly shaped and/or hollow. These errors were quantified for trees in central Amazonia after adjusting the number of trees sampled in each class based on the diameter distribution of a large inventory. For large trees (DBH \geq 50 cm) total basal area was overestimated by 30%, while the overestimate was 11% for all trees with DBH \geq 5 cm. The total bole volume per hectare was overestimated by 11.2% (\sim 40 m³/ha). Most of this volume correction is attributed to the non-circular form of the cross section; the effect of hollow areas on the volume of the bole was only 0.7%. For trees above 31.8 cm DBH, which is the minimum diameter in the Projeto RADAMBRASIL inventories, the volume per hectare was overestimated by 4.4% using conventional measurements. Because of compensating errors in commonly used formulas, however, the volume overestimate associated with conventional methods does not imply biomass overestimation in studies that have used the RADAMBRASIL dataset.

Keywords: irregularities of the bole, volume of the bole, hollow trees, basal area, biomass.

1. Introduction

Estimates of emissions of greenhouse gases from deforestation and logging in Brazilian Amazonia are derived from estimates of biomass obtained from large-scale inventories of wood volume. Occurrence of irregular and hollow boles can directly affect the estimates of volume and of greenhouse gas emissions from the region. This is because measures of diameter, basal area and wood volume invariably treat the bole as a solid of revolution, making the assumption that any cross section of the bole is circular (Ahrens and Holbert, 1981). In tropical forests, trees with indentations and irregularly shaped boles lead to overestimates in the measures of basal area and volume when using a measuring tape, even when diameter is measured above any buttresses or protuberances (Clark, 2002; Clark and Clark, 2000; Sheil, 1995). The errors are larger in species that have accentuated irregularities in the bole, such as *Aspidosperma discolor* A.DC. (Carapanaúba) and *Minquartia guianensis* Aubl. (Acariquara), and in large trees, which tend to have more irregularities and higher frequencies of hollow trunks (Clark and Clark, 2000; Fearnside, 1992, 1997a).

The occurrence of hollow trunks can also mean significant overestimates in measurements of basal area and of real wood volume, this being one of the uncertainties in estimates of biomass and of carbon emissions based on forest inventories (Brown and Lugo, 1992; Fearnside, 2000). Hollow trees are important in forest-management plans and are associated with the presence of termites (Amelung et al., 2002) and treefalls caused by wind and lianas (Putz et al., 1983); these affect turnover rate, average stand age, and rates of gap formation and consequent recruitment of pioneers. For Amazonia, estimates of hollow volume have varied from 1.6% to 9.2% of the total volume of the boles per unit of area (Fearnside, 1992, 1997b, 2000; Brown et al., 1995; Brown and Lugo, 1992).

Irregular and hollow boles will not influence biomass estimates that are based on direct weighing of trees or on allometric equations derived from directly weighed trees, but these characteristics of the boles will affect biomass estimates derived from commonly used wood volume data. In this paper we evaluate the effect of irregularities in the bole and the occurrence of hollow trunks on the measurements diameter and basal area for trees in Amazonia. These findings have important implications for estimates of forest volume and biomass and for carbon emissions from deforestation.

2. Materials and Methods

2.1. Collection site

The collection areas were six sites spread over \sim 45 km² in the Tarumã Small-Farmer Rural Settlement Project, centered about 50 km northwest of Manaus, Amazonas, Brazil (60.16°W; 2.83°S). Average annual precipitation is 2075 mm, with July to September being $<$ 100 mm/month; mean altitude is 100 m; mean monthly temperature ranges from 26 °C to 27.6 °C (INMET, 2003). The vegetation is dense upland rain forest without seasonal flooding, on nutrient-poor yellow latosol (Oxisol)(Magnago et al., 1978; Yamazaki et al., 1978). The six sites chosen were in primary forest, without recent natural gaps or growth of pioneers associated with

1 deforestation borders. The area is a new colonization front (< 5 years old) and deforestation for
 2 agriculture was authorized by the Brazilian Institute for the Environment and Renewable Natural
 3 Resources (IBAMA). A total of 303 trees (DBH \geq 5 cm) were felled in the field at random, but
 4 following pre-defined quotas by size class. An inventory of 72 ha (Castilho, 2004) was then used
 5 to adjust the felled sample using a distribution of tree diameters normally found in forests
 6 (diameter classes 5-cm DBH intervals). The numbers used to adjust the frequency of sampled
 7 trees to match that found in the forest are based on the 72 ha inventoried by Castilho (2004) and
 8 are termed “replication factors” in this paper (Table 1).

9
 10 [Table 1 here]

11 2.2. Evaluation of circumference measures for obtaining the volume of the bole.

12
 13 For the 303 trees botanical samples were collected and disks of constant thickness (~3
 14 cm) were removed with a chainsaw. Disks were taken at breast height and at the top of the bole,
 15 below the thickening associated with the base of the first major branch. For 73 trees chosen
 16 randomly from the full sample of 303 trees, two additional disks were taken, positioned at 33%
 17 and 66% of the length between breast height and the height of the first major branch. For all trees
 18 measurements were made of total height, height of the bole and circumference as determined
 19 with a measuring tape at each disk-sampling point. The measurements at breast height were
 20 made 1.36 m above the ground or above the buttresses, if present. Each disk’s outline was drawn
 21 on a large sheet of paper by tracing the outer edge and inner hollows if present. The drawings
 22 were affixed to a flat wall and photographed with an 80-mm lens from a standard distance of 4 m
 23 using a digital camera. The average pixel size in the digital photographs was 1.876 mm on each
 24 side, determined using four reference marks on the wall. The view angle was perpendicular and
 25 scale varied by only 0.6% from the center to the edge of the panel.

26 Using Adobe Photoshop 4.0 software (Adobe Systems, Inc., 1996) all of the pixels were
 27 selected that corresponded to areas with wood, using the image with amplification of 600%. The
 28 area was determined in pixels, converted to square centimeters and compared with the cross-
 29 sectional area obtained by the conventional method, which considers the perimeter taken with a
 30 measuring tape in the field to be the circumference of a perfect circle and without any hollows.
 31 Three corrected biometric attributes for each tree (diameter, basal area and volume) were
 32 calculated from the true area of sections of the bole, as determined by the pixel count, thereby
 33 correcting for the effects of non-circular shape and hollow trunks. The corrected diameter would
 34 be, for example, the diameter calculated for a perfect circle with an area equal to that determined
 35 by the pixel count of the section cut from a tree. Oval sections, irregularities and the presence of
 36 hollow areas mean that the “conventional” biometric attributes will be larger than the “corrected”
 37 attributes (Figure 1 and Table 2).

38 From the corrected cross-sectional areas, the volume of each bole was calculated using
 39 the Smalian formula: $\{(A_{si} + A_{sf}) / 2\} \times h$; where A_{si} = area of the cross section at breast height,
 40 A_{sf} = height at the top of the bole; and h = height of the commercial bole. This procedure was
 41 adopted for the 73 trees for which cross sections were sampled at four positions along the bole,
 42 and also for the other 230 trees for which cross sections were only sampled at breast height and
 43 near the first large branch.

44 45 2.3. Botanical identification

46
 47 Herbarium vouchers from each tree were identified by practical botanical experts
 48 (parabotanists) who were employees of the herbarium of the National Institute of Research in the
 49 Amazon (INPA). For the 303 trees sampled randomly, 186 different species or morpho-species
 50 were identified. Voucher specimens are kept at INPA.

51 52 **3. Results**

53 54 3.1. Effect of non-circular form and of hollows on conventional estimates of diameter, basal area 55 and wood volume

56
 57 For species with irregularities in the bole, the conventional measurements of basal area
 58 can overestimate by up to 400% the real cross-sectional area of wood with bark at breast height
 59 (Figure 1 and Table 2). When the sample of 303 trees was adjusted to represent the true
 60 frequency distribution of diameter classes in *terra firme* (upland) forest in central Amazonia, the

1 corrected diameter was, on average, 3.7% smaller at breast height and 3.1% smaller at the top
 2 of the bole, when compared with the diameter obtained in the conventional way (from
 3 determining the girth with a measuring tape and assuming this value to be the circumference of a
 4 circle).

5
 6 [Figure 1 and Table 2 here]
 7

8 The overestimate in the diameter measures caused by the non-circular shape and hollow
 9 trunks is greater for large trees (Figure 2a). For trees with DBH \geq 50 cm, adjusted to their
 10 frequency in a large inventory (*i.e.*, “inventory-adjusted” by use of the replication factors; see
 11 Table 1), the mean conventional DBH was 14.5% larger than the mean corrected DBH; about
 12 half of this effect was caused by six trees with very irregular boles, most of which are illustrated
 13 in Figure 2b. These six trees had conventional DBH that varied from 45 to 92 cm. At the top of
 14 the bole, the average overestimate of the diameter was 8.6% for the same size class (DBH \geq 50
 15 cm). The cross section becomes more circular in higher parts of the bole.

16
 17 [Figure 2 here]
 18

19 By the conventional method, the inventory-adjusted basal area/ha was 11% larger than
 20 the corrected basal area. The six trees with very irregular boles were responsible for about one-
 21 third of this effect. Inventory-adjusted mean overestimate of the area of the disk per tree was
 22 6.6% at breast height and 6% at the top of the bole (Figure 3). The error is again greater for large
 23 trees. For trees with DBH \geq 50 cm, the overestimate of the cross-sectional area at breast height
 24 averaged 30%, about half of this (14%) being caused by the six trees with very irregular boles.
 25 The median overestimate of basal area was only 12% for all trees $>$ 50 cm DBH.

26
 27 [Figure 3 here]
 28

29 Considering all trees with DBH \geq 5 cm, conventional measurements resulted in a mean
 30 overestimate per inventory-adjusted tree of 6.5% in the volume of the bole and of 11.2% in the
 31 bole volume per hectare. This is an overestimate of about 40 m³/ha. Again, about one-third of
 32 this (4%) was due to the six large trees with highly irregular cross sections. For trees with DBH
 33 \geq 50 cm (n = 23) the inventory-adjusted overestimate of stand bole volume was of 24%, half of
 34 this being due to the six highly irregular trees. The 23 large trees were also responsible for
 35 almost half of the error per hectare, or approximately 24 m³/ha. The difference in the estimate of
 36 volume was again greater for larger trees (Figure 4). The trees with the largest overestimates of
 37 volume using conventional measures of diameter were: *Minquartia guianensis* Aubl. (common
 38 name Acariquara, DBH = 45.8 cm), 65.6% overestimated volume; *Chimarrhis turbinata* DC.
 39 (Madeira-do-Remo, DBH = 92.5 cm), 94%; *Aspidosperma discolor* A.DC. (Carapanaúba, DBH
 40 = 52.2 cm), 105.1%; *Aspidosperma discolor* A.DC (Carapanaúba, DBH = 61.6 cm), 130.6%; and
 41 *Swartzia polyphylla* DC. (Paracutaca, DBH = 86.4 cm), 320.7%.

42
 43 [Figure 4 here]
 44

45 The volumetric estimate obtained with conventional DBH and the formula (eq. 1) used by
 46 Projeto RADAMBRASIL (1978-1983; sheet 20A, volume 18, p. 17), when compared with the
 47 “corrected” (Smalian) volume, was 6.3% larger (inventory-adjusted mean per tree), considering
 48 only those trees above the minimum diameter inventoried by RADAMBRASIL (31.8 cm DBH).
 49 For volume per hectare of trees with DBH \geq 31.8 cm, the overestimate was only 4.4% (n = 93
 50 prior to replication). This is much smaller than the 15.3% overestimate found for bole volume
 51 per hectare for trees with DBH \geq 31.8 cm calculated by the Smalian method and conventional
 52 DBH .

$$53 \quad V = \pi/4 \times DBH^2 \times H \times FF \quad (eq. 1)$$

54
 55 Where:

56 V = Volume with bark (m³)

57 DBH = Diameter at breast height (m)

58 H = Commercial height (m)

59 FF = Form factor: 0.7.

60
 61

3.2. Occurrence of hollow trees

Hollow areas of different sizes were found in only 30 of the 303 trees sampled (Table 3). The lowest disk (taken at 1.36 m or above any buttresses) was the most frequent location for hollows. But at this height, only 7.7% of the sampled trees had hollows and these, when present, occupied an average of only 9% of the cross-sectional area. In just 3.2% of the sampled trees, hollow areas were found at the top of the bole. Only one of the 303 trees had hollow area at both the top of the bole and at breast height, possibly being hollow along the entire length of the bole.

The sum of the individual basal areas of all trees indicates that the hollow areas at breast height or just above the buttresses occupied only 1.1% of the total cross-sectional area of the sample. At the top of the bole, the hollow area represented 0.8% of the total area at this height for all trees. Hollows larger than 30% of the cross-sectional area of the bole were not found at any height. With respect to the total area of the cross section of the bole, 24 of the 303 trees had hollow areas that occupied up to 10% of the cross-sectional area; in 8 trees hollows occupied 10 to 20%, and in 5 trees the hollow area occupied 20 to 30%.

[Table 3 here]

For the sampled trees, hollow trunks were more frequent in trees with larger diameters (Figure 5). When the occurrence of hollow areas was ignored, volume was overestimated by only 0.6% in the 303 sampled trees and the bole volume per hectare was overestimated by 0.7% for all trees, as compared to the volume obtained from DBH corrected for the effects of irregularities and hollows (Smalian formula). This is because hollow areas occur mainly in large trees, and these did not need to be replicated when adjusting to inventory frequencies.

[Figure 5 here]

4. Discussion

4.1. Effect of non-circular cross section and of hollow trunks on measures of diameter, basal area and wood volume

The effects of irregularities of the bole and of buttresses on estimates of diameter, basal area, volume and biomass have been evaluated in tropical forests (Clark, 2002; Clark and Clark, 2000; Sheil, 1995), but there are no studies that separate the effects buttresses and of non-circular shapes (including those above any buttresses). Discussion in the literature has focused on the effects of buttresses and hollows as sources of bias in measures of biometric attributes, with possible effects on biomass estimates. Indeed, diameter measures at breast height in trees with buttresses have been the source of intense debate on the apparent temporal trend of increasing biomass in permanent plots of Neotropical forests (Clark, 2002; Clark and Clark, 2000), increasing the list of uncertainties concerning the role of tropical forests as a source or a sink of carbon (Houghton, 2003). The occurrence of hollow trunks has also been considered as a bias towards overestimation in biomass calculations, up to 9% being discounted in recent estimates of carbon emissions (Fearnside, 2000).

The results of the present study point to new considerations: (i) the irregular form of the boles of the large trees and species with accentuated indentations can lead to overestimation of biometric attributes, (ii) the occurrence of hollow trunks seems to cause little error in the estimates of wood volume. For the first effect, and at the stand level, the importance of irregularities in the bole will be highly sensitive to the stand density of species with very irregular boles and to the greater effect of irregularities in large trees. Forests with high density of species with irregular boles can contain an important bias towards overestimation. The errors caused by irregularities and hollow trunks are more important for forest biomass than the average bias per tree would suggest because the biases are more accentuated in the large trees that represent a substantial amount of wood volume per hectare. In spite of the forests of central Amazonia having less biomass in large trees, as compared to other areas in Amazonia (see Chave et al., 2001), the percentage reaches 23% in trees with DBH \geq 50 cm according to an estimate of biomass in 20 ha in central Amazonia (do Nascimento, 2002).

On the other hand, the difference between conventional and corrected stand volume cannot be applied in a simple fashion to correct stand biomass estimates downward. This is because allometric regressions relate conventional DBH to true stand biomass in felled and weighed samples. Therefore, the independent variable that must be used in biomass estimates is the conventional (not the corrected) DBH. Biomass errors in a forest inventory can be in either

1 direction, depending on how the importance of irregularities and hollows in that inventory
2 compares with the (unfortunately unknown) importance of these factors in the felled and
3 weighed trees used to derive allometry.

4 Commercial volume is based on large trees and will be overestimated using geometric
5 formulas (such as equation 1). The correction factor is both greater and more uncertain for large
6 trees (Figures 2a, b). The error can be minimized if the volumes of species with very irregular
7 boles are estimated separately. Large-scale inventories carried out in Amazonia, such as Projeto
8 RADAMBRASIL, included species with highly irregular boles in their volume estimates. The
9 Smalian formula, based on the conventional measurements of diameter or circumference, has
10 been applied to obtain volumes used as reference values in developing and validating models
11 (Ribeiro, 1996, p. 23; Moura, 1994, p. 29; Higuchi and Ramm, 1985, p. 35; Fernandes et al.,
12 1983, p. 539). Naturally, the errors will be smaller in the models in which the dependent variable
13 was obtained using only species with boles that were more regular and free of defects, as
14 assumed by Fernandes et al. (1983). Such models are appropriate for commercial wood species,
15 but not for estimating the total volume per unit area in a community. Species with very irregular
16 boles also generate significant amounts of waste when logged, and volumetric models developed
17 for commercial logging always result in overestimates for these species.

19 4.2. Hollow trees

21 Hollows were more frequent and were larger toward the base of the bole. In only one of
22 the 303 trees was a hollow area found at both ends of the bole. In the 73 trees sampled at four
23 positions, no hollows were found in the slice 2/3 of the way up the bole. However, the number of
24 observations was too small to make inferences about the continuity of hollows in every bole,
25 since hollows were found in only 10% of the trees. Considering all trees that were hollow at
26 breast height, among the 303 trees in the study, the total hollow area would be equivalent to a
27 single bole of just 25 cm diameter. The effect of hollows on bole volume was determined by
28 transforming trees into thinner volumes of revolution using the true cross-sectional area of wood
29 at the position of each disk, then applying the Smalian formula. The effect of hollows on the total
30 bole volume per hectare was small: a reduction of only 0.7%. This observation will increase the
31 estimates of carbon emission from deforestation in Amazonia, such as those of Fearnside (1992,
32 1997b, 2000), which used Projeto RADAMBRASIL data and discounted by 6.6-9.2% for hollow
33 boles. However, the percentage found here is close to that reported by Brown and Lugo (1992).
34 For RADAMBRASIL data, these authors assumed, that hollows occupy 2% of the total bole
35 volume/ha, giving a 1.6% downward correction for stand biomass estimates by assuming that
36 20% of the boles with $DBH \geq 40$ cm are hollow up to 2 m above the ground. A similar
37 percentage was found by Clark and Clark (2000) in tropical forest plots in Costa Rica, where the
38 hollow area was estimated at 1.7% of the total volume of boles with diameter above 30 cm. For
39 open forests in Rondônia, Brown et al. (1995) found hollow areas in less than 20% of 53 boles
40 examined and estimated that the total hollow volume at less than 4%. These numbers indicate
41 that the occurrence of hollow areas can, in fact, represent little bias in the biomass estimates.
42 However, it should be pointed out that in the study in question the estimate of 0.7% hollow
43 volume (only in the volume of the bole) is indirect because the height of each hollow area was
44 not appraised along the length of the bole. For trees with DBH over 40 cm, the percentage of
45 hollow areas found in this study (13%) was much smaller than the 27% reported for central
46 Amazonia by Fearnside (1997b), based on N. Higuchi (personal communication). For trees over
47 10 cm DBH ($n = 145$), an even higher percentage (32%) was reported by Rodrigues and Valle
48 (1964) for trees of sandy soil forests in central Amazonia.

50 4.3. Effect of non-circular and hollow trunks on the biomass estimates

52 The results reported here do not affect biomass estimates that are based on direct
53 weighing of trees or on allometric equations derived from weighed trees. However, estimates of
54 wood volume in inventories could be overestimated but have this bias offset by other variables
55 used in the formula that is adopted for the biomass estimate. A more detailed explanation can
56 clarify this result.

57 The biomass estimates carried out starting from volumetric data are based on forest
58 inventories that are the only available sources of data with broad spatial representativeness
59 (Brown and Lugo, 1992; Brown et al., 1989, 1991), according to the model:

$$61 \text{ TAGB} = \text{Inventoried volume} \times \text{VEF} \times \text{WD} \times \text{BEF} \quad (\text{eq. 2a})$$

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Where:

TAGB = Total above-ground biomass of standing trees ≥ 10 cm DBH (Mg ha^{-1}),

Inventoried volume = Commercial volume of the boles above inventoried minimum DBH ($\text{m}^3 \text{ha}^{-1}$),

VEF = Volume expansion factor, representing the volume of boles of trees with DBH between 10 cm and the minimum inventoried DBH,

WD = Wood density (g cm^{-3});

BEF = Biomass expansion factor (adds the biomass of the crown, for all trees ≥ 10 cm DBH).

The above model has been used to obtain biomass estimates per hectare for Brazilian Amazonia starting from RADAMBRASIL inventories that, as demonstrated, report overestimated values of wood volume due to irregularities and hollow trunks. However, it is necessary to evaluate how the effects of irregularities and hollow trunks reported in the present study will influence estimates of biomass and of carbon emissions.

The variables in equation 2a assume the following values, according to Houghton et al. (2001), Brown (1997), Brown & Lugo (1992) and Brown et al. (1989):

VEF = 1.25 for dense forests and 1.5 for other Amazonian forests;

WD = 0.69 g cm^{-3} ;

BEF = $\exp\{3.213 - 0.506 \text{ Ln SB}\}$, for $\text{SB} < 190 \text{ Mg ha}^{-1}$;

BEF = 1.74, for $\text{SB} > 190 \text{ Mg ha}^{-1}$;

SB = Stand biomass (biomass of boles ≥ 10 cm DBH) = Inventoried volume \times VEF \times WD

Brown (1997, p. 6) presents another equation (eq. 2b), which is included here for comparison with the approach of Houghton et al. (2001):

$$\text{TAGB} = \text{VOB} \times \text{WD} \times \text{BEF} \quad (\text{eq. 2b})$$

Where:

TAGB = Total above-ground biomass of standing trees ≥ 10 cm DBH (Mg ha^{-1})

WD = Wood density;

BEF = Biomass expansion factor (adds crown biomass, for all trees ≥ 10 cm DBH),

VOB = Volume over bark of the boles of all trees ≥ 10 cm DBH ($\text{m}^3 \text{ha}^{-1}$).

Estimates of "total above-ground biomass (TAGB)" based on Brown and Lugo (1992), in the equations above (2a, b), only refer to the live-tree component ≥ 10 cm DBH. For estimates of TAGB, it has been suggested that the equation may result in bias due to the occurrence of hollow trunks (Fearnside and Laurance, 2003) when using the model of Brown and Lugo (1992), or Houghton et al. (2001). However, in a recent publication, Fearnside and Laurance (2004) eliminate the corrections originating from hollow areas, and conclude that the volume estimates based on Brown et al. (1989) do not need corrections for this factor. Corrections for irregularities in the bole are not needed when adopting the model of Brown and Lugo (1992). First, it is necessary to review the development of three models:

$$\text{BEF} = \exp\{3.213 - 0.506 \text{ Ln SB}\}, \text{ for } \text{SB} < 190 \text{ Mg ha}^{-1} \quad (\text{eq. 3})$$

$$\text{BEF} = 1.74, \text{ for } \text{SB} > 190 \text{ Mg ha}^{-1}; \quad (\text{eq. 4})$$

$$\text{BEF} = \text{TAGB} \times (\text{SB})^{-1} \quad (\text{eq. 5})$$

The model in equation 5 was the basis for obtaining the coefficients presented in equation 3 and the constant value of BEF in equation 4. It was based, in 1989, on the "known" values of TAGB and SB for 32 plots in humid forest, almost all in Venezuela (Brown et al., 1989). The known values of TAGB were actually indirect estimates derived using allometric models for individual trees, starting from D, H and WD (diameter at breast height, total height and wood density, respectively), according to equation 6:

$$\text{Dry biomass} = 0.0899 (\text{D}^2 \times \text{H} \times \text{S})^{0.9522} \quad (\text{eq. 6})$$

The values of SB were also estimated using D (measured in the field), commercial H (measured in the field), form factor of 0.7, and WD, this last being obtained from tables for 65%

1 to 85% of the species in the 32 inventories, or, in the case of the species with unknown WD,
2 from the average of WD of the known species.

3 Because many estimates of Amazonian biomass are ultimately derived from the
4 Venezuelan data (*e.g.*, equation 6), the interpretation of any errors in the estimate of SB (biomass
5 of all boles ≥ 10 cm DBH) starting from the 32 inventories in Venezuela is critical. TAGB in the
6 Venezuelan data can be presumed to have been estimated without bias, but the volume used in
7 obtaining SB was apparently overestimated by assuming that the bole is a perfect solid of
8 revolution. However, this will not create a bias in the estimate of TAGB at other sites (such as
9 the inventories of RADAMBRASIL in Brazilian Amazonia) because the same volume
10 overestimate occurs in these other inventories. BEF, based on correct TAGB and SB
11 overestimated in the 32 plots in Venezuela, would compensate for similar errors in the estimate
12 of SB in the RADAMBRASIL inventories. In other words, in determining the BEF any
13 consistent bias in the value of SB is compensated for in the adjustment of the regression derived
14 by Brown (equations 3 and 4). In the case of the 32 plots, Brown et al. (1989) obtained BEF =
15 1.74 (95% CI = 0.08) from the biomasses of the individual trees in the 32 plots as estimated
16 using the allometric relationship for individual trees described in equation 6. Later, Brown and
17 collaborators considered plots with lower TAGB and obtained equation 3 to estimate BEF
18 starting from SB and TAGB. Therefore, there is no reason to expect bias in the estimate of
19 commercial volume (or SB) in the plots studied by Brown and collaborators; since the volume
20 (and therefore SB) of the boles inventoried was also overestimated by RADAMBRASIL, there
21 will not be bias in the final estimate of TAGB when applied to the RADAMBRASIL data.
22

23 5. Conclusions

24
25 Irregularly shaped and hollow boles lead to significant errors in measurements of bole
26 volume in central Amazonia. These errors result in an overestimate of 11.2% in the total bole
27 volume per hectare. For RADAMBRASIL inventories, tree volume per hectare was
28 overestimated by 4.4%. The additional effect of hollow trunks is only 0.7%. Both effects are
29 greater in large trees, which tend to have more irregular boles and higher frequencies of hollow
30 trunks. The effect of irregularities is related to the occurrence and distribution of tropical species
31 that have boles with accentuated indentations. Tree hollows and irregularities are highly species-
32 specific; therefore the data and conclusions in this study may not be representative of other
33 tropical forests. The effect of these factors on stand biomass in each forest will depend on the
34 abundance of species with accentuated irregularities. In spite of these errors being present in the
35 stand volume tables of the RADAMBRASIL inventories, compensating errors in the formulas
36 used to interpret volume data mean that there is no net bias in biomass calculations from such
37 stand volume tables based on widely used equations (*e.g.*, Brown et al., 1989; Brown and Lugo,
38 1992).
39

40 Acknowledgments

41
42 We thank the National Council for Scientific and Technological Development (CNPq
43 AI470765/01-1) and the National Institute for Research in the Amazon (INPA PPI I-3620) for
44 financial support. Three reviewers contributed valuable comments.
45

46 6. References

- 47
48 Adobe Systems, Inc. 1996. Adobe Photoshop. Version 4.0. Adobe Systems, Inc. San Diego,
49 California, U.S.A.
50
51 Ahrens, S.; Holbert, D. 1981. Uma função de forma de tronco e volume de *Pinus taeda* L.
52 *Boletim de Pesquisa Florestal* 3, 37-68.
53
54 Amelung, W.; Martius, C.; Bandeira, A. G.; Garcia, M. V. B.; Zech, W. 2002. Lignin
55 characteristics and density fractions o termite nests in Amazonian rain forest – indicators
56 of termite feeding guilds? *Soil Biology & Biochemistry* 34, 267-372.
57
58 Brazil, Projeto RADAMBRASIL. 1978. Folha SA.20, Levantamento de Recursos Naturais.
59 Manaus. Vol. 18. Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.
60 747 pp
61

- 1 Brown, I. F.; Martinelli, L. A.; Thomas, W.; Moreira, M. Z.; Ferreira, C. A.; Victoria, R. A.
2 1995. Uncertainty in the Biomass of Amazonian Forests: an Example from Rondônia,
3 Brazil. *Forest Ecology and Management* 75, 175-189.
4
- 5 Brown, S. 1997. Estimating biomass and biomass change of tropical forest: A Primer. *Forestry*
6 *Paper 134*, Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
7 55 pp.
8
- 9 Brown, S.; Gillespie, A. J. R.; Lugo, A. E. 1991. Biomass of tropical forests of South and
10 Southeast Asia. *Canadian Journal of Forest Research* 21, 111-117.
11
- 12 Brown, S.; Gillespie, A. J. R.; Lugo, A. E. 1989. Biomass estimation methods for tropical forest
13 with applications to forest inventory data. *Forest Science* 35(4):881-902.
14
- 15 Brown, S.; Lugo, A. 1992. Aboveground biomass estimates for tropical moist forest of the
16 Brazilian Amazon. *Interciencia* 17(1), 8-18.
17
- 18 Castilho, C. V. 2004. Variação espacial e temporal da biomassa arbórea viva acima do solo em
19 uma floresta de terra-firme na Amazônia central. Doctoral thesis in ecology, Instituto
20 Nacional de Pesquisas da Amazônia/Fundação Universidade Federal do Amazonas,
21 Manaus, Amazonas, Brazil. 72 pp.
22
- 23 Chave, J.; Riéra, B.; Dubois, M. A. 2001. Estimation of biomass in a neotropical forest of French
24 Guiana: Spatial and temporal variability. *Journal of Tropical Ecology* 17:79-96.
25
- 26 Clark, D. B. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term
27 plot data. *Ecological Applications* 12, 3-7.
28
- 29 Clark, D. B.; Clark, D. A. 2000. Landscape-scale variation in forest structure and biomass in a
30 tropical rain forest. *Forest Ecology and Management* 137, 185-198.
31
- 32 do Nascimento, H. E. M. 2002. *Biomassa Total Acima do Solo e a Fragmentação de Floresta de*
33 *Terra-firme na Amazônia central*. Doctoral thesis in ecology, Instituto Nacional de
34 Pesquisas da Amazônia/Fundação Universidade Federal do Amazonas. Manaus,
35 Amazonas, Brazil. 98 pp.
36
- 37 Fearnside, P. M. 1992. Forest biomass in Brazilian Amazônia: Comments on the estimate by
38 Brown and Lugo. *Interciencia* 17(1), 19-27.
39
- 40 Fearnside, P. M. 1997a. Wood density for estimating forest biomass in Brazilian Amazonia:
41 *Forest Ecology and Management* 90, 59-87.
42
- 43 Fearnside, P. M. 1997b. Greenhouse gases from deforestation in Brazilian Amazonia: net
44 committed emissions. *Climatic Change* 35, 321-360.
45
- 46 Fearnside, P. M. 2000. Global warming and tropical land-use change: greenhouse gas emissions
47 from biomass burning, decomposition and soils in forest conversion, shifting cultivation
48 and secondary vegetation. *Climatic Change* 46, 115-158.
49
- 50 Fearnside, P. M.; Laurance, W. F. 2003. Comment on "Determination of deforestation rates of
51 the world's humid tropical forests". *Science* 229, 1015a.
52
- 53 Fearnside, P. M.; Laurance, W. F. 2004. Commentary: Tropical deforestation and greenhouse-
54 gas emissions. *Ecological Applications* 14(4), 982-986.
55
- 56 Fernandes, N. P.; Jardim, F. C. S.; Higuchi, N. 1983. Tabelas de volume para floresta tropical de
57 terra-firme da Estação Experimental de Silvicultura Tropical do INPA. *Acta Amazonica*
58 13(3-4), 537-545.
59
- 60 Higuchi, N.; Ramm, W. 1985. Developing bole wood volume equations for a group of tree
61 species of central Amazon (Brazil). *Commonwealth Forestry Review* 64(1), 33-41.

- 1
2 Houghton, R. A. 2003. Why are estimates of the terrestrial carbon balance so different? *Global*
3 *Change Biology* 9, 500-509.
4
- 5 Houghton, R. A.; Lawrence, K. T.; Hackler, J. L.; Brown, S. 2001. The spatial distribution of
6 forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change*
7 *Biology* 7(7), 731-746.
8
- 9 INMET, 2003. *Instituto Nacional de Meteorologia*. www.inmet.gov.br. Accessed 12 Aug. 2003.
10
- 11 Magnago, H.; Barreto, R. A. A.; Pastore, U. 1978. *Projeto RADAMBRASIL*, Folha SA.20, Parte
12 IV-Vegetação. Rio de Janeiro, Brazil. pp. 413-530.
13
- 14 Moura, J. B. 1994. *Estudo da forma do fuste e comparação de métodos de estimativa*
15 *volumétrica de espécies florestais da Amazônia brasileira*. Masters Thesis, Universidade
16 Federal do Paraná. Curitiba, Paraná, Brazil. 114 pp.
17
- 18 Putz, F. E.; Coley, P. D.; Lu, K.; Montalvo, A.; Aiello, A. 1983. Uprooting and snapping of
19 trees: structural determinants and ecological consequences. *Canadian Journal of Forestry*
20 *Research* 13, 1011-1020.
21
- 22 Ribeiro, R. J. 1996. *Estudos de função de forma para espécies florestais de terra-firme da*
23 *Amazônia*. Masters dissertation in tropical forest science, Instituto Nacional de Pesquisas
24 da Amazônia/Fundação Universidade do Amazonas, Manaus, Amazonas, Brazil. 76 pp.
25
- 26 Rodrigues, W. A.; Valle, R. C. 1964. *Ocorrência de troncos ocos em mata de baixio da região*
27 *de Manaus, Amazonas*. Pub 16, Botânica, Instituto Nacional de Pesquisas da Amazônia,
28 Manaus, Amazonas, Brazil. 8 pp.
29
- 30 Sheil, D. 1995. A critique of permanent plot methods and analysis with examples from Budongo
31 Forest, Uganda. *Forest Ecology and Management* 77, 11-34.
32
- 33 Yamazaki, D. R.; Costa, A. M. R.; Azevedo, W. P. 1978. *Projeto RADAMBRASIL*, Folha SA.20,
34 Parte III-Pedologia. Rio de Janeiro, Brazil. pp. 247-410.

1 FIGURE LEGENDS

2

3 **Figure 1.** Cross sections of boles of trees included in Table 2: **A.** *Swartzia polyphylla* DC.
 4 (Paracutaca); **B.** *Chrysophyllum sanguinolentum* (Pierre) Baehni ssp. *spurium* (Ducke) T. D.
 5 Penn. (Leitera), and **C.** *Pouteria cladantha* Sandwith (Abiurana).

6

7 **Figure 2. A.** Conventional DBH assuming a circular cross section is plotted against the corrected
 8 DBH, which is the diameter of a circle having the true area of the cross section determined from
 9 disk tracings. All but the six species with highly irregular boles shown in panel **B** are included.

10 **B.** Irregular trees: (a) *Astronium lecointei* Ducke, (b) *Miquartia guianensis* Aubl., (c)
 11 *Aspidosperma discolor* A. DC., (d) *Aspidosperma discolor* A. DC., (e) *Swartzia polyphylla* DC.,
 12 and (f) *Chimarris turbinata* DC.

13

14 **Figure 3.** Conventional versus corrected DBH for large trees (DBH \geq 40 cm; n = 52). One tree
 15 was excluded for which the correction was approximately -400%. Circle symbols represent the
 16 section at breast height (1.36 m) and “x” symbols represent the section at the end of the bole. The
 17 plot shows clearly that the magnitude of the correction increases at larger tree diameters and that
 18 the relationship has high variability.

19

20 **Figure 4.** Estimated volume of the bole decreases when the corrected DBH is used. The
 21 correction and the variance of the correction are both greater for larger trees. Paired symbols for
 22 each tree show the effect of correcting only for cross section shape (open circles) and the effect
 23 of correcting for both shape and hollows (x symbols).

24

25 **Figure 5.** Frequency of hollow trees by diameter class.

Table 1. Number of trees sampled by size class and replication factors to emulate known stem density in central Amazonia.

Conventional DBH	Number of trees sampled	Replication factor	Stems/ ha
≥5 - <10	36	19.8	714
≥10 - <15	45	5.6	253
≥15 - <20	52	2.6	136
≥20 - <25	41	1.9	77
≥25 - <30	37	1.3	47
≥30 - <35	27	1.1	30
≥35 - <40	15	1.5	22
≥40 - <45	17	1.0	17
≥45 - <50	13	1.0	13
≥50 - <55	3	2.0	6
≥55 - <60	6	1.0	6
≥60 - <65	3	1.0	3
≥65 - <70	2	1.0	2
≥70 - <75	1	1.0	1
≥75 - <80	1	1.0	1
≥80 - <85	0	-	0
≥85 - <90	2	1.0	2
≥90 - <95	1	1.0	1
≥95 - <100	0	-	0
≥100 - <105	0	-	0
≥105	1	1.0	1
Total	303	-	1332

Table 2. Cross sections of boles of trees found in the dense forests of central Amazonia with areas determined by two methods: (1) mean assuming that DBH obtained in the field refers to a circular section and (2) corrected area determined by counting pixels and subtracting internal hollow areas. Cross sections of these species are illustrated in Figure 1.

Species:	A. <i>Swartzia polyphylla</i> DC. (Paracutaca);	B. <i>Chrysophyllum sanguinolentum</i> (Pierre) <i>Baehni</i> ssp. <i>spurium</i> (Ducke) T. D. Penn. (Leitera)	C. <i>Pouteria cladantha</i> Sandwith (Abiurana)
(1) Conventional area (cm ²)	5865.8	319.9	630.3
(2) Corrected area (cm ²)	1133.1	252.0	555.9
Overestimate (%)	417.7	26.9	13.4

Table 3. Tree species with hollow boles.

Scientific name
<i>Aniba panurensis</i> (Meisn.) Mez
<i>Aniba williamsii</i> O.C. Schmidt
<i>Astronium lecointei</i> Ducke
<i>Bocoa viridiflora</i> (Ducke) R.S. Cowan
<i>Botryarrhena pendula</i> Ducke
<i>Caryocar</i> sp.
<i>Chimarrhis turbinata</i> DC.
<i>Chrysophyllum sanguinolentum</i> (Pierre) Baehni ssp. <i>spurium</i> (Ducke) T. D. Penn.
<i>Cupania scrobiculata</i> Rich.
<i>Duguetia surinamensis</i> R.E. Fr.
<i>Eschweilera grandiflora</i> (Aubl.) Sandwith
<i>Eschweilera rodriguesiana</i> S.A. Mori (3 hollow trees)
<i>Eschweilera</i> sp.
<i>Licania sothersiae</i> Prance
<i>Licania</i> sp.
<i>Manilkara cavalcantei</i> Pires & W.A. Rodrigues ex T.D. Penn.
<i>Micropholis mensalis</i> (Baehni) Aubrév.
<i>Minuartia guianensis</i> Aubl.
<i>Ouratea discophora</i> Ducke
<i>Pouteria anomala</i> (Pires) T.D. Penn.
<i>Pouteria caimito</i> (Ruiz & Pav.) Radlk.
<i>Pouteria</i> sp.
<i>Protium grandifolium</i> Engl.
<i>Salacia</i> sp.
<i>Swartzia corrugata</i> Benth.
<i>Tovomita</i> sp.
<i>Virola</i> sp.
<i>Zygia juruana</i> (Harms) L. Rico
Unidentified (1 hollow tree)

Figure 1

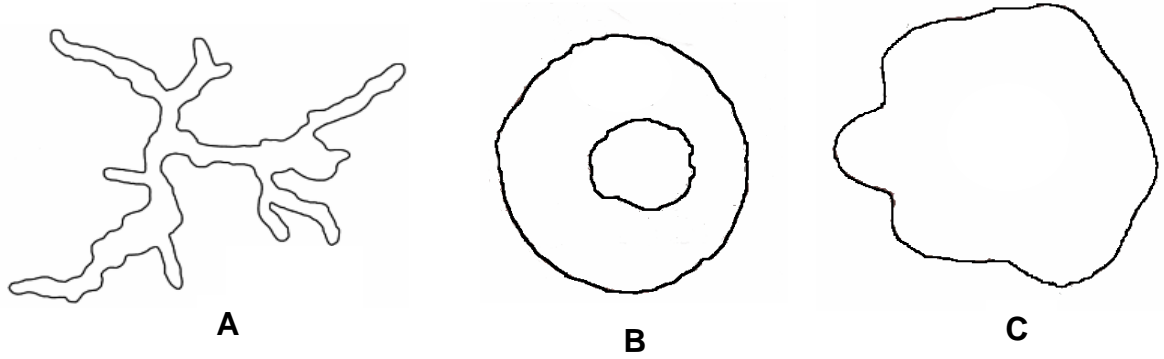


Figure 2A

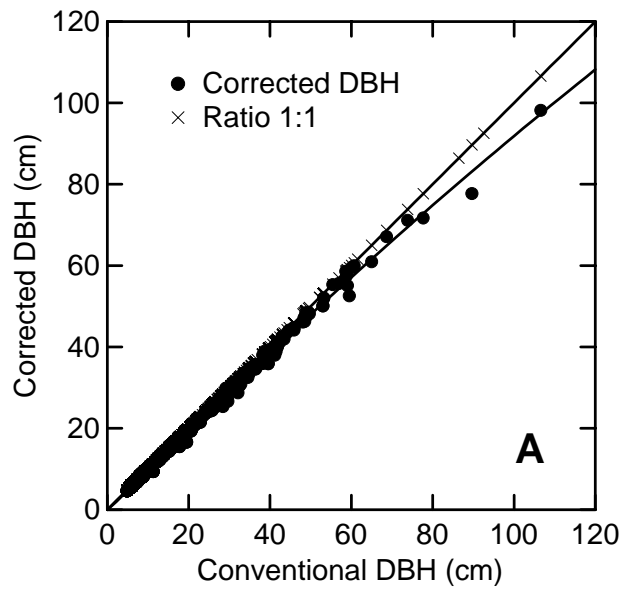


Figure 2 B

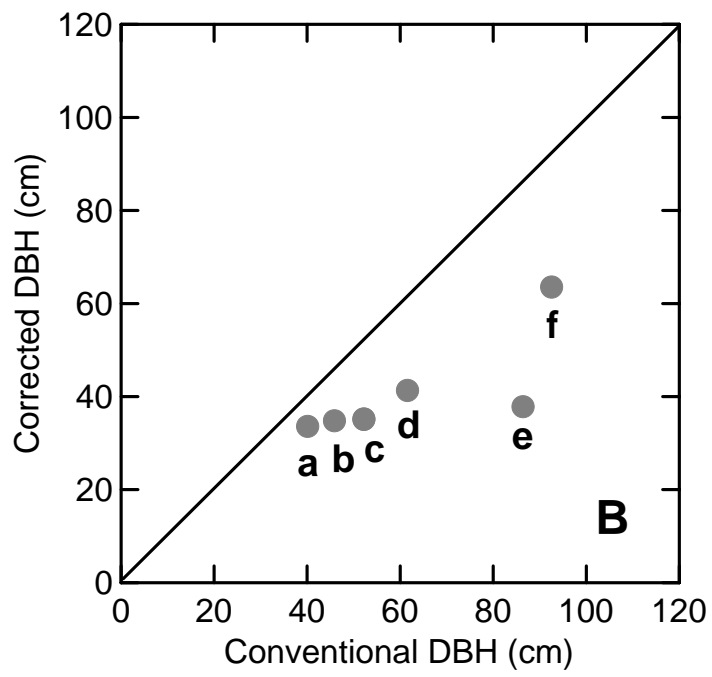


Figure 3.

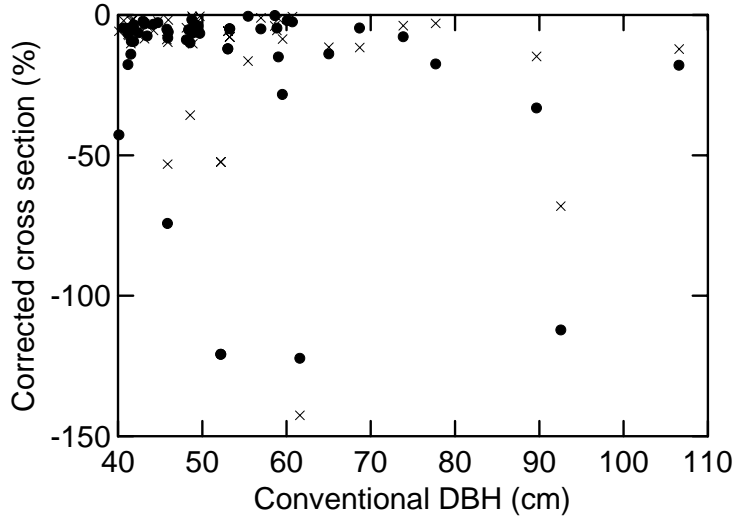


Figure 4.

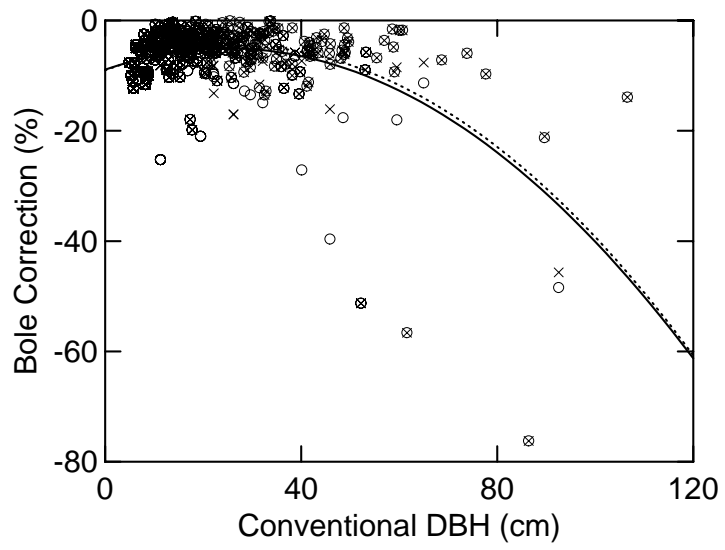


Figure 5.

