ELSEVIER

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 184 (2003) 355–368

Forest Ecology and Management

www.elsevier.com/locate/foreco

Analysis of alternative methods for estimating carbon stock in young tropical plantations

Christopher J. Losi[a,*], Thomas G. Siccama[a], Richard Condit[b], Juan E. Morales[b]

[a]*Yale School of Forestry and Environmental Studies, 205 Prospect St., New Haven, CT 06511, USA*
[b]*Smithsonian Tropical Research Institute, Unit 0948, APO AA, 34002-0948, USA*

Received 19 July 2002; received in revised form 12 September 2002; accepted 7 April 2003

Abstract

Estimates of carbon stock in forest plantations are generally based on allometric equations relating either carbon or biomass to diameter at breast height (DBH). These equations are usually based on measurement of the fresh mass of each tree with sub-samples taken to determine moisture content to convert to dry weight. However, drying time and the number of sub-samples varies between studies. Furthermore, the carbon concentration of different tree parts is rarely measured directly, but generally assumed to be 50% of dry weight.

This study analyzed those assumptions and determined their effect on regression equations and on species-specific stand level estimates of carbon stock for *Anacardium excelsum* and *Dipteryx panamensis* growing in 7-year-old mixed-species plantations in Panama. Four methods were used to develop aboveground carbon estimates for the same sample of trees. Results indicated that the drying time, the number of sub-samples taken, and whether or not carbon was measured directly had only a small effect on the estimate of carbon stock for the entire cohort of trees. None of the methods developed using the same sample of Panamanian trees gave stand level estimates of carbon stock that differed by more than 10% from the best estimate for either species.

Another sample of slightly larger *D. panamensis* trees growing in 5- and 6-year-old mixed-species plantations in Costa Rica [J. Trop. For. Sci. 13 (3) (2001) 450] was used to develop a second set of regression equations. We hypothesized that a regression equation would give a more accurate estimate of carbon stock if the range of tree sizes used to produce the regression more closely matched the range of sizes that the regression was being applied to. When the Costa Rican equation developed using the full range of trees was compared to a Panamanian equation developed using the full range of tree diameters that we sampled, the estimates of carbon stock for the Panamanian plantation differed by 10.2%. However, when two additional regression equations were created using the range of tree diameters that overlapped, the estimates of carbon stock for the Panamanian plantation differed by only 5.2%, supporting our hypothesis.

Keywords: Carbon sequestration; Techniques; Carbon; Biomass; Allometric equations

1. Introduction

Increased establishment of tree plantations on cleared land in the tropics has long been suggested as a way of reducing the rate of increase in atmospheric

---

[*] Corresponding author. Present address: Allegheny National Forest, Bradford District, HC 1 Box 88, Bradford, PA 16701, USA. Tel.: +1-814-362-4614; fax: +1-814-368-8116.
E-mail address: closi@fs.fed.us (C.J. Losi).

0378-1127/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0378-1127(03)00160-9

CO_2 (Dyson, 1977). As trees grow, they sequester carbon in their tissues, and as the amount of tree biomass increases (within a forest or in forest products) the increase in atmospheric CO_2 is mitigated. The ability of these plantations to sequester carbon has received renewed interest, since carbon sequestration projects in developing nations could receive investments from companies and governments wishing to offset their emissions of greenhouse gases through the Kyoto Protocol's Clean Development Mechanism (Fearnside, 1999).

A good estimate of carbon sequestration is essential to any project of this type. The rate of carbon sequestration in live tree biomass is computed by finding the difference between the carbon stock of a population of trees at two different ages. Estimates of carbon stock are generally produced by first measuring the total biomass of the population using one of two approaches. The first is to estimate wood volume for each tree using a volume equation, convert wood volume to mass using an estimate of timber density, and then convert wood mass to total tree biomass using a biomass expansion factor. The other approach is to apply a regression equation that directly converts external measurements, such as stem diameter and sometimes height, to total tree biomass. Individual tree biomass values produced using either approach are summed to produce the biomass of the entire population, which is then multiplied by a standard value of carbon concentration to produce an estimate of the carbon stock.

While the first approach to estimating carbon stock is useful where volume estimates already exist (as in actively managed forests), the second approach requires fewer steps to estimate carbon stock once a regression has been prepared. On the other hand, developing allometric regressions requires estimating carbon content and/or biomass of individual trees, a task that involves multiple steps. Furthermore, there is no universal standard for estimating the biomass or carbon of a tree.

The general procedure for estimating biomass is to cut down a tree, weigh it, take samples of different tree components, and dry these components. The biomass (dry weight) of the tree is then calculated by applying the moisture loss of the samples to the entire tree. Depending on the researcher, however, the number of samples taken from a tree will vary. Nelson et al. (1999) dried a single sample of the bole at breast height, while Kraenzel et al. (2003) dried a separate sample for each meter of the bole's length. Moreover, the drying time and temperature varies between researchers. Nelson et al. (1999) dried samples at 105 °C until constant weight was reached while Kraenzel et al. dried the wood for 1 week at 70 °C. Other researchers (Likens and Bormann, 1970) have dried samples at 80 °C.

Most researchers estimate carbon by assuming the carbon content of dry biomass to be a constant 50% by weight (Brown, 1986; Montagnini and Porras, 1998). However, other authors have used a carbon concentration of 45% by weight (Whittaker and Likens, 1973). Occasionally, carbon is measured directly by burning the samples in a carbon analyzer (Kraenzel et al., 2003).

Another issue relates to the range of tree sizes used to develop allometric regressions. Researchers often caution that regressions should not be applied to trees whose sizes are outside the range of trees that were used to develop the regressions, so a large range of diameters is ideal for calculating regressions. Yet a population of trees (especially those growing in plantations) may only have a small range of diameters. Assuming that the population is within the range used to develop the regression, would a regression developed from a narrower range of diameters be more accurate in predicting the carbon stock of that population than a regression developed from a larger range of diameters? We predict that it would.

Our goal was to test how carbon estimates for a population of trees depended on methods chosen for measuring individuals. We measured trees of two species using four different methodologies that vary in the number of bole samples taken, the temperature and duration of drying, and the biomass-to-carbon conversion. The four sets of carbon estimates were then used to develop regressions that relate carbon content of an individual tree to its diameter at breast height (DBH). Finally, the four regressions were applied to a population of trees and different estimates of total carbon stock were produced.

We also compared the estimates based on our own regressions to alternative estimates based on regressions developed using data from a published study (Shepherd and Montagnini, 2001; Shepherd and Montagnini, unpublished data). The data collected by

Shepherd and Montagnini included trees well beyond the range of sizes found in our population. As a result, we were able to test whether recomputing their regressions using a narrower range of tree sizes would produce a more accurate estimate of carbon stock.

2. Methods

2.1. Site description

Data was collected from 42 plantation plots established in September 1993 in central Panama. Five tree species—*Anacardium excelsum*, *Dipteryx panamensis*, *Enterolobium cyclocarpum*, *Hura crepitans*, and *Swietenia macrophylla* were planted in mixed-species plots near the villages of Los Hules (9.05°N, 79.92°W), Las Pavas (9.1°N, 79.88°W), and Cerro Cama (9.03°N, 79.90°W). Climate data are available at a meteorological station on Barro Colorado Island, 20 km from all of the study plots. Barro Colorado belongs to the "tropical moist forest" life zone (Croat, 1978), has an annual temperature range from 21° to 31°, an average annual rainfall of about 2500 mm, and an intense 4-month dry season during which little rain falls (Leigh, 1999).

Trees were planted 2 m apart in a square grid. A plot consisted of a 10 m × 10 m grid with five individuals each of five species. Individuals of a given species were spread out within plots so that each row or column generally had only one individual of each species. Notwithstanding these constraints, species arrangements were purposely varied from plot to plot. Around each plot, one or two border rows were planted to reduce edge effects. Initially, 45 plots were established, 42 on private lands belonging to five different farmers, with 3–15 plots on each property. Three additional plots were established on government land within the former Panama Canal Zone; however, all three were destroyed by fire during the dry seasons of 1994–1996.

Only two of the five species growing in the mixed-species plots were analyzed in this paper. Measurement and analysis of alternative methods for estimating tree and stand carbon mass were undertaken using *A. excelsum* and *D. panamensis* because we believed that regression equations developed for these species would be the most useful to other authors. Two species, *S. macrophylla* and *E. cyclocarpum* were infested by pests and were so deformed that they barely grew (see Fig. 1). Regressions equations for these species would only have been applicable to very small trees. A third species, *H. crepitans* had the largest diameters but short, flat-topped crowns positioned well below the dominant *A. excelsum* and *D. panamensis*. It appeared that future plantations of *H. crepitans* would need to be pruned intensively or planted at a higher density, both of which could change the shape (and therefore the allometric relationships) of the trees.

2.2. Tree selection

Trees used in this analysis were from across the size range in the plantations. In June and July 2000, DBH was measured for all *D. panamensis* and *A. excelsum* individuals in plots as well as those in internal border rows (border rows surrounded on both sides by a plot). Height was also measured on one individual of each species in each plot. The same cohort of trees had also been measured when they were 2 years old, in August 1995 (Losi, 1996).

Individuals of each species were selected for harvesting using a stratified sample with two strata. The upper stratum consisted of N_u trees in the largest two thirds of the population (based on DBH). The lower stratum consisted of trees with DBH values that were within the range of DBH values measured on 2-year-old trees in 1995 (about 7–8%).

Nine trees were harvested from the upper stratum using a systematic sample. The trees in this stratum were assembled in a list sorted from smallest to largest DBH and divided into 9 consecutive substrata with $N_u/9$ trees plus one substratum containing the remainder of $N_u/9$ trees. The nth tree in each substratum (where a single integer value of n was chosen randomly for each species) was then harvested. For both species, the random value chosen for n was larger than the 10th substratum, meaning that only nine individuals of each species were chosen in this stratum.

Five individuals were harvested from the lower stratum using a simple random sample without replacement. These five smaller trees were selected to improve the precision of the estimate of carbon stock for 2-year-old trees.

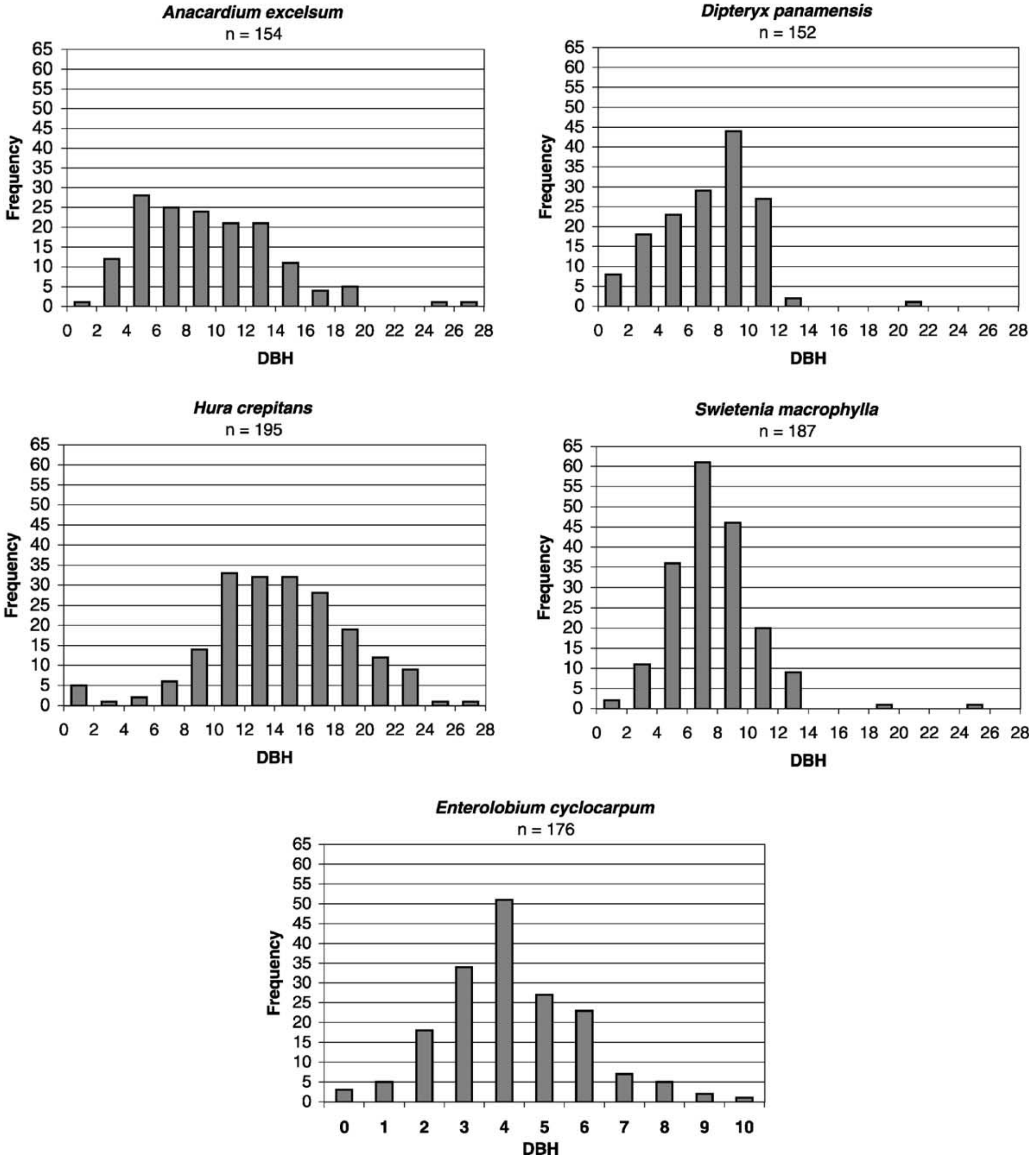

Fig. 1. Diameter distribution of *A. excelsum*, *D. panamensis*, *H. crepitans*, *S. macrophylla*, and *E. cyclocarpum*. For the first four species, histograms show the number of trees in 2 cm DBH size classes (0–2, 2–4 cm, etc.). Due to their smaller size, *E. cyclocarpum* trees are displayed in 1 cm size classes (<0.5, 0.5–1.5, 1.5–2.5 cm, etc.). Forty-five plots, with five individuals of each species, were planted in 1993. Three plots were destroyed by fire and were eliminated from our analysis. The number of trees still living in 2000 (out of a possible 210) is displayed in each histogram (*n*).

Selection of trees for harvest was done without regard to the ownership of the land; however, the sample resulted in at least one tree of each species being selected from each farm. Out of deference to the wishes of the property owners, the largest tree of each species was not harvested on any farm. Farmers were paid for the trees that were harvested.

Harvesting took place over 3 weeks in July and August 2000. DBH was measured immediately before felling since some growth had occurred since the initial measure. Height was measured after felling. The tree was separated into five different components: bole, branches, dead wood, twigs, and leaves; and weighed on a portable hanging scale. Twigs were defined as the current season's growth; generally they were green and had leaves. Since the trunk was not perfectly vertical, the bole was identified as all wood with a living cambium that led up to the highest point on the tree. The bole was cut into 2 m sections, which were then weighed. Branches were defined as all wood with a living cambium that was not otherwise classified as twigs or bole.

2.3. Sample processing

After the entire tree had been weighed in pieces, samples were taken from each tree component. Ten leaves were chosen at random from each tree, without regard to leaf area. A 5 cm slice of wood was taken from the bottom of each 2 m bole section. Ten twig pieces were selected by first randomly selecting 10 twigs without regard to size, cutting them into pieces 5 cm long, and selecting 10 pieces at random from this sample. Dead wood was sampled in the same way. Branches were broken into straight segments, then sampled from thickest to thinnest: segments were sorted by diameter, placed in a line, and about ten 5 cm long pieces were collected at equally spaced intervals from the entire line of branches. This ensured that a wide range of branch thicknesses was sampled.

Samples for each component were pooled, sealed in plastic bags, and transported to a laboratory in Panama City where they were weighed on a scale accurate to 1 g (large samples) or 0.01 g (small samples). Samples were dried over heating elements in a drying room at 70 °C for about a week (6–8 days) and weighed again. All samples were then transported to New Haven, Connecticut where they were processed in two batches.

We had originally intended to compare the amount of moisture lost using the most aggressive drying method (105 °C to constant weight) with the least aggressive drying method (70 °C to constant weight) found in the literature. Unfortunately, the first batch (consisting of all component samples from nine *A. excelsum* and five *D. panamensis*) underwent partial oxidation after being left in ovens for several months at 105 °C. Although no flame was observed, the color of the wood became noticeably darker and later tests showed that these pieces had lost carbon as a result of the "drying" process. As a result, the first batch was discarded and we abandoned all attempts at 105 °C. We instead used 80 °C as our most aggressive method and obtained the data from the second batch (five *A. excelsum* and nine *D. panamensis*). Although not all trees were represented in this batch, a total of 123 samples were analyzed.

Before processing the second batch, samples were weighed to account for the moisture that had been absorbed since removing from the 70 °C ovens in Panama. A portion of each sample was then ground to pass through a 0.5 mm screen (1.0 mm screen for leaves), so that it could be analyzed for percent carbon on a LECO® CHN-600 analyzer. The unground portion of the sample was placed back into an oven at 80 °C and dried to constant weight.

2.4. Estimating carbon for individual trees

We used four different methods to determine the carbon content of each tree sampled. Methods differed in the way in which carbon was estimated for each piece of wood or component sample (Table 1). Once an estimate of carbon content was made for each piece of wood or component sample, an estimate was made of the amount of carbon present in the component. Finally, the components were summed to produce an estimate of carbon content for that tree.

2.4.1. Method 1

This method measured carbon directly using the LECO® analyzer. For pieces of the tree that were ground and passed through the LECO® analyzer (the second batch), the carbon content of the piece was equal to the product of $M_{\mathrm{dir}} \times [C_{\mathrm{dir}}]$, where M_{dir} was

Table 1
Summary of the four methods used to measure the carbon content of individual trees[a]

Method number	Number of bole samples considered	Drying procedure	C concentration method
1	Multiple pieces, taken at 2 m increments	Dry 1 week at 70 °C in Panama, acclimate to ambient temperature in USA	Measured directly by LECO® CHN Analyzer
2	Multiple pieces, taken at 2 m increments	Dry 1 week at 70 °C in Panama, dry to constant weight at 80 °C in USA	50% dry weight
3	Multiple pieces, taken at 2 m increments	Dry 1 week at 70 °C in Panama	50% dry weight
4	Single piece, taken at 2 m	Dry 1 week at 70 °C in Panama, dry to constant weight at 80 °C in USA	50% dry weight

[a] Samples of each component (bole, branches, dead wood, twigs, and leaves) were taken from each tree, but we varied the number of bole samples that we considered. The carbon concentration specified in rightmost column was multiplied by the dry weight produced using the method in the third column to determine the carbon content of each component sample.

the mass of the piece before it was sub-sampled for direct carbon determination and $[C_{\mathrm{dir}}]$ was the C concentration measured for that same piece. For pieces that were discarded after undergoing partial oxidation (the first batch), the carbon content was estimated by $M_{1\,\mathrm{week}} \times \mathrm{CF_C}$, where $M_{1\,\mathrm{week}}$ was equal to the weight of the sample after drying for 1 week in Panama and CF_C was the appropriate component-specific correction factor for C concentration. $\mathrm{CF_C}$ was produced by computing $(M_{\mathrm{dir}}/M_{1\,\mathrm{week}}) \times [C_{\mathrm{dir}}]$ for each piece that was passed through the LECO® analyzer and then finding the average value for each component.

2.4.2. Method 2

This method assumed that C concentration was 50% of the dry weight of each component. Pieces were dried to constant weight at 80 °C in New Haven after being sub-sampled for carbon determination. No additional weight loss was observed during the last week of drying. The dry weight of pieces that underwent partial oxidation was determined by multiplying the weight of the piece after drying for 1 week in Panama by a component-specific correction factor. The correction factor represented the amount of weight that was expected to be lost if that piece were dried to constant weight at 80 °C.

2.4.3. Method 3

This method also assumed that C concentration was 50% of the dry weight of each component. Method 3 used the weight of each sample after drying for 1 week in Panama as the biomass. Since all samples were dried under these conditions there was no need to apply any correction factors.

2.4.4. Method 4

This method also assumed that C concentration was 50% of the dry weight of each component. Method 4 determined the biomass of the entire bole using dry weight of the bole section taken at 2 m. All other bole samples were ignored. The dry weight of 2 m bole sections that underwent partial oxidation was determined using a correction factor based on the average moisture loss of all other 2 m bole sections. Carbon contents of the other components were computed in the same way as Method 2 using the same number of samples as in Method 2.

2.5. Model development

Allometric models were created for each species by relating the carbon content of each tree to DBH. A different model was created for each of the four methods for measuring carbon. Each model was named with a code corresponding to the species and the method used to measure carbon content (e.g. Model A1 was developed for *A. excelsum* using Method 1 data, Model D3 was developed for *D. panamensis* using Method 3 data, etc.). An additional model for each species was created that related Method 1 carbon estimates to DBH and height (A1h and D1h). In order to keep the number of models manageable, carbon estimates using other methods

Table 2
Regression models for estimation of above-ground biomass of *A. excelsum* and *D. panamensis*[a]

Model name	Source of carbon estimate (tree sizes based on DBH)	Regression model	Symbol	Value	Standard error	r^2	Average unsigned deviation (%)	Significance level of *t*-value
A. excelsum								
A1	Method 1	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−3.4931	0.0983	0.9957	8.9	0.0000
			α	2.4843	0.0470			0.0000
A1h	Method 1	$\ln(C) = c + \alpha\ln(DBH)$	c	−3.7179	0.2227	0.9962	8.6	0.0000
		$+\beta\ln(H)$	α	2.1936	0.2633			0.0000
			β	0.4132	0.3684			0.28 (NS)
A2	Method 2	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−3.4577	0.1007	0.9955	9.2	0.0000
			α	2.4889	0.0482			0.0000
A3	Method 3	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−3.4278	0.1007	0.9955	9.2	0.0000
			α	2.4830	0.0482			0.0000
A4	Method 4	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−3.4877	0.1075	0.9950	9.7	0.0000
			α	2.5143	0.0515			0.0000
D. panamensis								
D1	Method 1	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.6344	0.0666	0.9975	7.1	0.0000
			α	2.5170	0.0363			0.0000
D1h	Method 1	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.8313	0.1010	0.9983	5.7	0.0000
		$+\beta\ln(H)$	α	2.1850	0.1442			0.0000
			β	0.4128	0.1752			0.0380
D2	Method 2	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.6362	0.0696	0.9973	7.5	0.0000
			α	2.5339	0.0379			0.0000
D2b	Method 2 (trees 8.4–11.2 cm)	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.2433	0.9620	0.8877	5.5	0.0801
			α	2.3661	0.4208			0.0049
D3	Method 3	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.6203	0.0699	0.9973	7.5	0.0000
			α	2.5327	0.0380			0.0000
D4	Method 4	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−3.3814	0.1213	0.9937	12.8	0.0000
			α	2.8643	0.0660			0.0000
S2	Shepherd and Montagnini (2001)	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.7450	0.5720	0.9385	9.4	0.0004
			α	2.6244	0.2125			0.0000
S2b	Shepherd and	$\ln(C) = c + \alpha\ln(\mathrm{DBH})$	c	−2.0619	0.6700	0.9544	4.8	0.0543
		Montagnini (2001)	α	2.3088	0.2914			0.0042
		(trees 8.4–11.2 cm)						

[a] In the models shown, c, α and β are coefficients, DBH is the diameter at breast height in cm, H is height in m, and C is total aboveground carbon content in kg. Tree size ranged from 2.4 to 18.6 cm DBH for *A. excelsum*, from 1.8 to 11.2 cm DBH for *D. panamensis* harvested in Panama, and from 8.4 to 16.2 cm for *D. panamensis* harvested in Costa Rica by Shepherd and Montagnini (2001). Two additional *D. panamensis* models were produced using the range of overlapping values (8.4–11.2 cm).

were not related to DBH and height for Methods 2, 3, and 4 in either species. All models are named and described in Table 2.

A final set of models was created using carbon measurements collected from 5- and 6-year-old *D. panamensis* growing in mixed-species plantations in Costa Rica (Shepherd and Montagnini, 2001, unpublished data). The trees were planted at 2 m × 2 m spacing (2500 stems/ha) and thinned twice to a final density of 625 stems/ha. Carbon measurements were based on 50% dry weight, and although the samples were dried at 70 °C, they were dried to constant weight, so the method of carbon determination was most similar to Method 2. Therefore, the model developed from 12 Costa Rican trees was called Model S2.

The range of sizes of trees harvested in Costa Rica (8.4–16.2 cm DBH) was different from the range harvested in Panama (1.83–11.2 cm). As a result, we were able to test whether developing a regression with a smaller range of trees would improve its accuracy. Model S2b was developed from the Costa Rica data but only included the five trees with DBH smaller than 11.2 cm (the maximum DBH used in the Panamanian models). Model D2b was developed from the Panamanian Method 2 data but only includes the six *D. panamensis* with diameters greater than 8.4 cm (the minimum DBH used in the Costa Rica model).

Following Nelson et al. (1999), the following indicators of goodness of fit were calculated for each model:

1. r^2 of the simple regression.
2. Standard error: reported for the intercept and for partial regression coefficients of the independent variables.
3. Significance of t-value: reported for each independent variable.
4. Average unsigned deviation: an indicator of the precision of the model in predicting individual tree biomass values. For each tree used in a regression, the difference between predicted dry weight and observed dry weight was expressed as a percentage of observed dry weight. The absolute values of all cases (deviations) were then averaged.

2.6. Stand estimates

The allometric models developed in this paper were used to estimate the amount of carbon present in each *D. panamensis* and *A. excelsum* in the 42 plots (border rows excluded). Individual tree estimates for all trees of a single species were then summed to produce cohort-level estimates. Since Models S2 and S2b did not include any *D. panamensis* smaller than 8.4 cm and our D series regressions did not include any trees larger than 11.2 cm, a separate set of cohort-level estimates was created. These estimates only included trees within the range of 8.4–11.2 cm and were calculated for Models D2, D2b, S2, and S2b.

For comparison between the methods, these cohort-level estimates were scaled up to estimates per hectare in a single species plantation. These estimates of metric tons per hectare (Mg/ha) constitute a ‘‘hypothetical plantation’’ and are not valid estimates for a single species plantation because competition effects in a single species plantation are different from mixed-species plantations.

3. Results

3.1. Tree size and survivorship

The average DBH of *A. excelsum* was slightly larger than *D. panamensis* (9.4 versus 7.5 cm), but heights of the sampled individuals were about the same (8.1 and 8.2 m, respectively). Fig. 1 shows basic size and survivorship statistics for all five species in the experimental plantation.

3.2. Comparison of carbon estimates

Measured carbon content of dry bole samples was 47.8% (0.7% S.D.) for *A. excelsum* and 48.5% (0.4% S.D.) for *D. panamensis*. Thus, for both species, Method 2 estimates, which assume carbon concentration to be 50% dry weight, were nearly always higher than direct estimates (Method 1; see Fig. 2). Carbon estimates based on a single week of drying (Method 3) were higher than estimates where trees were dried to a constant weight (Method 2); both were higher than direct estimates (Method 1). Finally, estimates made using only one stem sample (Method 4) were higher than direct estimates, except in the two *D. panamensis* that were smaller than 5 cm.

We found that the percent moisture content of a bole sample varied inversely with the position on the bole where the sample is taken. For every tree that was dried to constant weight, the moisture content was found to be lower at the ground than at the highest bole section that was measured on the tree. When bole slices for all trees of a given species were combined, a relationship was observed between distance from the ground and moisture content; however, a closer relationship was observed between diameter of the bole

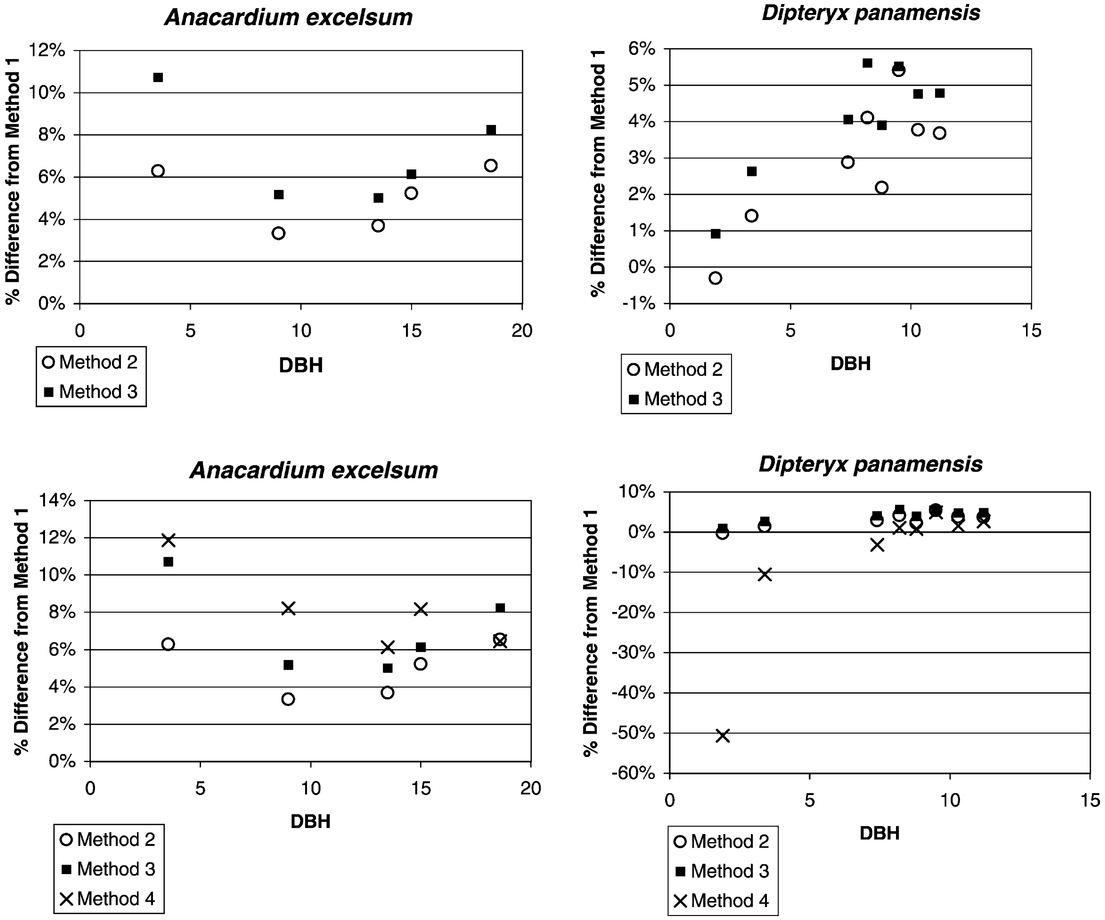

Fig. 2. The effect that the method of carbon determination has on carbon values for individual trees. Only trees for which pieces were passed through the carbon analyzer and dried to constant weight are shown. Each point shows the difference between the carbon value for a single tree determined using Methods 2, 3 or 4 and the carbon value for that same tree computed using Method 1. For clarity, the first two scatter plots are shown without carbon values produced using Method 4.

slice and moisture content. Diameter of the bole slice was also found to be positively related to the carbon content of the piece (Fig. 3).

3.3. Comparison of models

Scatter plots in Fig. 4 indicate a strong nonlinear relationship between Method 1 data and DBH. However, in order to facilitate comparison to linear models in other papers (Nelson et al., 1999), DBH and carbon estimates given by all four models were ln-transformed, and linear regressions were fit to the ln-transformed data.

Regressions of carbon content on DBH, with ln-transformed data, do an excellent job of predicting the carbon content of individual trees. Aside from Model D2b, all r^2 values for models developed with our data were above 99%, while the two regressions based on data from Costa Rica had r^2 values above 90% (see Table 2). The coefficient for height was not significant in Model A1h, but it was significant at the 10% level for all other coefficients in all other models. The average unsigned deviation for Model D4 was 12.8%, however, all other models had an average unsigned deviation of less than 10%.

Aside from the models that incorporate height, there is little variation among models developed for the same species (Table 2). These models have the format $\ln(C) = c + \alpha \ln(\mathrm{DBH})$, where C is the total

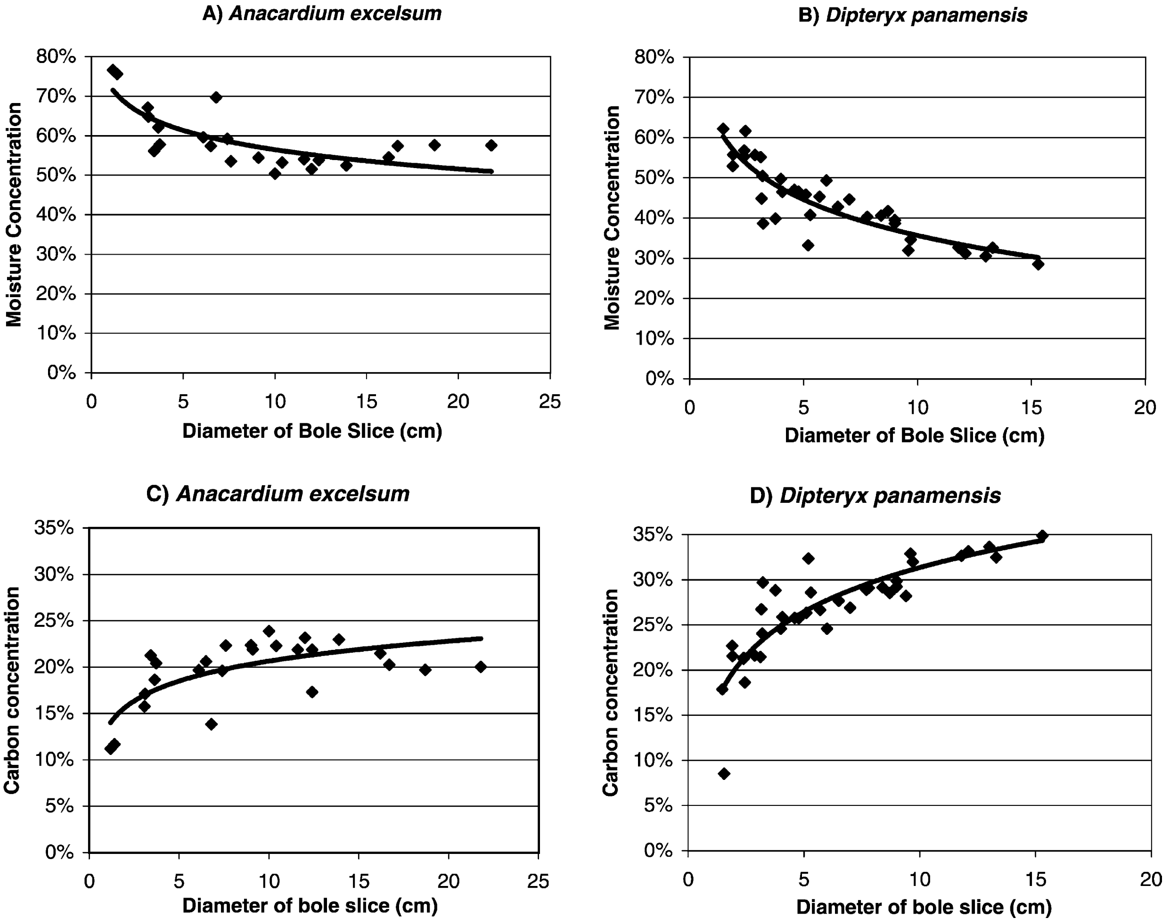

Fig. 3. Scatter plots for *A. excelsum* and *D. panamensis* indicate a relationship between the moisture concentration of a bole section ($[M_b]$) and the diameter of that bole section (D_b), as shown by the following regressions: (A) $[M_b] = -0.0705\ln(D_b) + 0.7270$, $r^2 = 0.5971$; (B) $[M_b] = -0.1288\ln(D_b) + 0.6531$, $r^2 = 0.7734$. A relationship was also found between the carbon concentration of a bole section ($[C_b]$) and D_b: (C) $[C_b] = 0.0310\ln(D_b) + 0.1350$, $r^2 = 0.4832$; (D) $[C_b] = 0.0706\ln(D_b) + 0.1510$, $r^2 = 0.7454$. Only bole sections with a diameter of at least 1 cm were used.

aboveground carbon content in kg and DBH is the diameter at breast height in cm. For *A. excelsum* models, the coefficient of the intercept (c) ranged from −3.49 to −3.43, and the coefficient of the dependent variable (α) ranged from 2.48 to 2.51. Clearly, this variation is not significant, since the standard error of the c coefficient is 0.1 for each model and the standard error of the α coefficient is 0.05 for each model. For *D. panamensis*, in models D1, D2, and D3, c ranged from −2.64 to −2.62 and α ranged from 2.52 to 2.53. Again, this variation is not significant, since the standard error of the c coefficient is 0.07 for each model and the standard error for the α coefficient is 0.04 for each model. Model D4, however, was clearly an outlier, with a c value of −3.38 and an α value of 2.86.

3.4. Comparison of carbon estimates

Using regression equation A1, the carbon stock of the *A. excelsum* cohort is estimated to have increased from 0.53 Mg/ha in 1995 to 21.4 Mg/ha in 2000, for an average annual sequestration rate of 4.18 Mg/ha per year. Using regression equation D1, the carbon stock of the *D. panamensis* cohort is estimated to have increased from 0.64 Mg/ha to 26.5 Mg/ha, for an average annual sequestration rate of 5.18 Mg/ha per

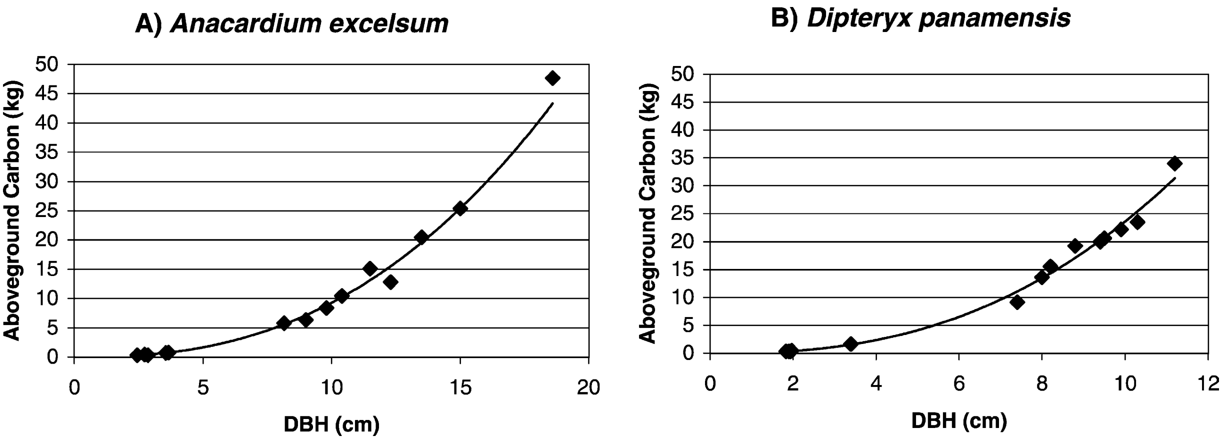

Fig. 4. Scatter plots for *A. excelsum* and *D. panamensis* indicate a strong nonlinear relationship between aboveground carbon content (determined using Method 1) and DBH, as shown by the following regressions: (a) $C = 0.0304(\mathrm{DBH})^{2.4843}$, $r^2 = 0.9957$; (b) $C = 0.0718(\mathrm{DBH})^{2.5170}$, $r^2 = 0.9975$, where C is total aboveground carbon content and DBH is diameter at breast height.

year. Again, these estimates of metric tons per hectare (Mg/ha) constitute a ‘‘hypothetical plantation’’ and are not valid estimates for a single species plantation because competition effects in a single species plantation are different from mixed-species plantations.

Table 3 shows carbon totals computed for the same cohort of trees measured in 2000 using the four basic models developed from our data set. Models developed using Method 1 produced the lowest values for each species. However, all carbon stock estimates produced using Models A1–A4 and Models D1–D4 were within 10% of each other.

Regression S2, based on data collected by Shepherd and Montagnini (2001) (Table 4) produced an estimate of carbon stock of 17.40 Mg/ha for the 8.4–11.2 cm portion of the population. This estimate is 10.2%

Table 3
Plantation-wide estimates of aboveground carbon stock for 7-year-old trees, produced using various models[a]

Model name	Model description	Carbon estimated when model applied to all *A. excelsum* (Mg/ha)	Change from A1 (%)	Change from A2 (%)
A. excelsum				
A1	C measured directly	21.42		
A2	50% dry weight	22.46	4.9	
A3	50% 1 week dry weight	22.78	6.4	1.5
A4	50% dry weight using 1 stem slice	23.29	8.8	3.7
Model name	**Model description**	**Carbon estimated when model applied to all *D. panamensis* (Mg/ha)**	**Change from D1 (%)**	**Change from D2 (%)**
D. panamensis				
D1	C measured directly	26.53		
D2	50% dry weight	27.52	3.7	
D3	50% 1 week dry weight	27.88	5.1	1.3
D4	50% dry weight using 1 stem slice	27.79	4.8	1.0

[a] Model names specified in this table correspond to models given in Table 2. The models were applied to all trees in the plantation plots (but not border rows). Data in columns marked ‘‘Change from *Model name*’’ is the percent difference between the estimate on that line and the estimate produced using *Model name*.

Table 4
The effect that the range of tree sizes used in a regression has on estimates of carbon stock produced by that regression[a]

Model name	Model description	Carbon estimated when model applied to *D. panamensis* 8.4–11.2 cm DBH (Mg/ha)	Change from D2 (%)	Change from D2b (%)
D2	50% dry weight	15.79		
D2b	50% dry weight (trees 8.4–11.2 cm DBH only)	15.96	1.1	
S1	50% dry weight following Shepherd and Montagnini (2001)	17.40	10.2	9.0
S1b	50% dry weight following Shepherd and Montagnini (2001) (trees 8.4–11.2 cm DBH only)	16.80	6.4	5.2

[a] All regressions were developed from *D. panamensis* growing in mixed-species plantations on abandoned farmland. Models starting with "D" are 7-year-old trees growing in Panama at 2500 stems/ha. Models starting with "S" are 5- or 6-year-old trees growing in Costa Rica that were planted at 2500 stems/ha and thinned on two occasions to a final density of 625 stems/ha (Shepherd and Montagnini, 2001). All models are applied to the same population of trees—trees in the Panamanian plantation plots with DBH between 8.4 and 11.2 cm.

greater than the D2 estimate for the same range of diameters (15.79 Mg/ha). However, when regression S2b, which was created using only the five Costa Rican trees that were between 8.4 and 11.2 cm, is applied to Panamanian trees within the same range of sizes, the carbon totals are only 6.4% greater than D2 and 5.2% greater than D2b.

4. Discussion

4.1. Comparison of carbon estimates made by models developed from the same data

For 7-year-old trees, Methods 2, 3, and 4 overestimated plantation-wide carbon totals (Table 3), but by less than 10%. The difference between per hectare carbon estimates produced by Method 1 versus those produced using Method 2 was <5% in both species. For many data applications, the additional accuracy afforded by determining carbon directly would not be worth the extra time and expense of grinding samples and running them through a carbon analyzer.

The discrepancy between Methods 1 and 2 can be attributed to the fact that Method 2 uses a carbon concentration of 50%. Our data show that the average carbon concentration of dry bole samples was approximately 48%, which falls between the 50% value used by Brown (1986) and the 45% value used by Whittaker and Likens (1973).

Only a small amount of additional water loss was observed after the first week of drying. In fact, the component-specific correction factor that was used in Method 2 to estimate the amount of additional moisture that was lost in partially oxidized pieces after the first week of drying (see Section 2.4.2) was greater than 0.96 for each component sample of each species. As a result, plantation-wide estimates calculated using regressions developed from Method 3 data are quite close to those calculated using regressions developed from Method 2 data (Table 3). After 1 week at 70 °C, any additional drying appears to have only a small effect on the accuracy of carbon estimates.

Nelson et al. (1999) found that taking a single stem sample at breast height (1.3 m) affected the final estimate of the tree's weight by less than ±4%. In this study, the carbon contents of both individuals of *D. panamensis* smaller than 5 cm DBH determined using Method 4 was more than 10% lower than the values determined using Method 1 (Fig. 2). Although Nelson found no relationship between tree size and the moisture content, when we pooled all of the bole slices for all trees of each species, we found a strong relationship between the moisture content and diameter in both species (Fig. 3). As this is a logarithmic relationship, the effect of diameter is greater for smaller diameters. For large trees, then, a single bole slice might do a good job of estimating the carbon content of the entire bole, and could explain the findings of Nelson et al.

One possible explanation for the variation in moisture content would be that the wood was not completely dried. Since larger pieces take longer to dry than small pieces, larger pieces would appear to have a higher dry weight. However, if this were the case, the carbon concentration of fresh wood would not be positively correlated with diameter. Yet, bole diameter explains nearly half of the variation between carbon concentrations for *A. excelsum* ($r^2 = 0.48$) and three-quarters of the variation between carbon concentrations for *D. panamensis* ($r^2 = 0.75$, see Fig. 3).

Our hypothesis is that moisture content of a bole cross-section is affected primarily by the proportion of young "living wood" (vascular cambium and phloem) in that cross-section. These living tissues tend to have higher water content than dead interior structural wood. Since the proportion of "living wood" is higher in bole sections with smaller diameters, they have a higher moisture content.

4.2. Comparison of carbon estimates made by models developed from different data

Although Models D2b and S2b were developed from different populations of trees growing in different countries, the estimations of carbon stock produced from these models only differ by 5.2% (Table 4) when applied to the range of trees that both models were developed from. Such a good agreement between these two estimates supports the conclusion of Fownes and Harrington (1992) that allometric regression models produced for the same species using the same range of tree sizes and similar methods will not vary much, even when trees are different ages and grown at different spacing. Differences in climate, spacing, and relative size (trees 8.4–11.2 cm were the largest trees in Panama and the smallest trees in Costa Rica) had only a minor effect on the models themselves.

The difference between estimates of *D. panamensis* carbon stock made using models developed from different populations and similar methods (Model D2b versus Model S2b; Table 4) is similar to the difference between estimates made using the same population of Panamanian data and different methods (Model D1 versus D2, D3, or D4; Table 3). In other words, the effect of the method used to compute carbon stock was about the same as the effect of the sample chosen.

By making the range of tree sizes used in the Costa Rica Model (Model S2) more similar to the range of tree sizes found Panama Models, we produced an estimate of carbon stock that was more similar to the estimates given by the Panama Models (Table 4). This fact suggests that models developed from a narrow range of diameters may be more accurate at predicting carbon stock for a population of trees in that range than a model developed from a wider range of diameters. Some authors (such as Brown, 1986) include a list of diameters and biomass estimates for each harvested tree that can be used for this purpose. Appendix A lists the amount of carbon contained in each tree and each tree component for all of the trees sampled in this paper.

Acknowledgements

This research was supported by grants from the Avina Foundation and the Tropical Resources Institute at Yale University. In-country logistical support was provided by the Center for Tropical Forest Science at the Smithsonian Tropical Research Institute and by Ecoforest S.A. This work could not have been completed without the cooperation of the Lorenzo, Martínez, Morán, Pérez and Soto families who provided the land for this plantation or without the help of the field assistants, especially Luis Pérez and Ruben Dario Ortega. Joel Tilley provided much-needed advice in the lab. We are grateful to Dan Shepherd for providing his data set for use in this analysis.

Appendix A.

Carbon contents of each tree sampled, computed using Method 1

DBH (cm)	Height (m)	Bole (kg of carbon)	Branches (kg of carbon)	Twigs (kg of carbon)	Dead branches and twigs (kg of carbon)	Leaves	Entire tree
A. excelsum							
2.5	3.22	0.26		0.01		0.05	0.32
2.7	3.6	0.31	0.01	0.03	0.00	0.06	0.41
2.9	3.2	0.25		0.03		0.05	0.33
3.6	4.45	0.58	0.05	0.02	0.01	0.06	0.73

Appendix A. (*Continued*)

DBH (cm)	Height (m)	Bole (kg of carbon)	Branches (kg of carbon)	Twigs (kg of carbon)	Dead branches and twigs (kg of carbon)	Leaves	Entire tree
3.7	4.45	0.65	0.02	0.03	0.01	0.05	0.77
8.2	8.35	4.04	1.06	0.13	0.14	0.39	5.76
9.0	7.72	4.36	0.98	0.16	0.12	0.71	6.32
9.8	9.03	5.37	1.61	0.15	0.04	1.19	8.36
10.4	8.92	6.85	1.78	0.40	0.24	1.17	10.43
11.5	9.96	8.75	3.73	0.57		2.06	15.11
12.3	9.88	9.12	1.91	0.33	0.64	0.81	12.82
13.5	8.42	10.84	6.10	0.64	0.07	2.81	20.45
15.0	12.25	17.75	3.19	0.93	0.21	3.32	25.40
18.6	14.44	31.07	9.33	1.69	0.67	4.92	47.67
D. panamensis							
1.8	2.33	0.25				0.07	0.32
1.9	2.42	0.26				0.09	0.35
1.9	2.65	0.28				0.06	0.34
2.0	3.05	0.41				0.05	0.46
3.4	5.31	1.30		0.04		0.28	1.62
7.4	7.35	7.04	1.30		0.03	0.76	9.13
8.0	9.11	9.17	2.51	0.23		1.70	13.60
8.2	11.58	12.22	1.49	0.10	0.56	1.16	15.53
8.8	10.05	12.47	4.68	0.23	0.48	1.40	19.26
9.4	8.36	11.31	5.13	0.83		2.69	19.96
9.5	9.62	13.65	4.47	0.16	0.89	1.40	20.58
9.9	10.2	13.56	4.94	0.49	0.54	2.65	22.17
10.3	9.29	14.34	6.09	0.12	0.46	2.45	23.48
11.2	10.42	21.04	8.50	0.37	1.73	2.36	34.00

References

Brown, S., 1986. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper 134. Food and Agriculture Organization of the United Nations, Rome.

Croat, T.R., 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, CA.

Dyson, F.J., 1977. Can we control the carbon dioxide in the atmosphere? Energy (Oxford) 2, 287–291.

Fearnside, P.M., 1999. Forests and global warming mitigation in Brazil: opportunities in the Brazilian forest sector for responses to global warming under the "clean development mechanism". Biomass Bioenergy 16, 171–189.

Fownes, J.H., Harrington, R.A., 1992. Allometry of woody biomass and leaf area in five tropical multipurpose trees. J. Trop. For. Sci. 4 (4), 317–330.

Kraenzel, M., Castillo, A., Moore, T., Potvin, C., 2003. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. For. Ecol. Manage. 173, 213–225.

Leigh Jr., E.G., 1999. Tropical Forest Ecology: A View from Barro Colorado Island. Oxford University Press, New York.

Likens, G.E., Bormann, F.H., 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Yale University School of Forestry Bulletin 79, 25 pp.

Losi, C.J., 1996. Carbon sequestration rates of five neotropical tree species and their feasibility for establishment in commercial plantations. Unpublished Undergraduate Thesis. Princeton University.

Montagnini, F., Porras, C., 1998. Evaluating the role of plantations as carbon sinks: an example of an integrative approach from the humid tropics. Environ. Manage. 22 (3), 459–470.

Nelson, B.W., Mesquita, R., Periera, J.L.G., Aquino de Souza, S.G., Batista, G.T., Couto, L.B., 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. For. Ecol. Manage. 117, 149–167.

Shepherd, D., Montagnini, F., 2001. Above ground carbon sequestration potential in mixed and pure tree plantations in the humid tropics. J. Trop. For. Sci. 13 (3), 450–459.

Whittaker, R.H., Likens, G.E., 1973. Carbon in the biota. In: Woodwell, G.M., Pecan, E.V. (Eds.), Carbon in the Biosphere, Proceedings of the 24th Brookhaven Symposium in Biology. United States Atomic Energy Commission, Upton, New York, pp. 281–302.