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Total carbon stocks in a tropical forest landscape of the Porce region, Colombia

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Abstract

Detailed ground-based quantifications of total carbon stocks in tropical forests are few despite their importance in science and ecosystem management. Carbon stocks in live aboveground and belowground biomass, necromass, and soils were measured in a heterogeneous landscape composed of secondary and primary forest. A total of 110 permanent plots were used to estimate the size of these carbon pools. Local biomass equations were developed and used to estimate aboveground biomass and coarse root biomass for each plot. Herbaceous vegetation, fine roots, coarse and fine litter, and soil carbon to 4 m depth were measured in subplots. In primary forests, mean total carbon stocks (TCS) were estimated as 383.7 ± 55.5 Mg C ha^{-1} ($\pm$S.E.). Of this amount, soil organic carbon to 4 m depth represented 59%, total aboveground biomass 29%, total belowground biomass 10%, and necromass 2%. In secondary forests, TCS was 228.2 ± 13.1 Mg C ha^{-1}, and soil organic carbon to 4 m depth accounted for 84% of this amount. Total aboveground biomass represented only 9%, total belowground biomass 5%, and total necromass 1% of TCS in secondary forests. Monte Carlo methods were used to assess the uncertainty of the biomass measurements and spatial variation. Of the total uncertainty of the estimates of TCS, the variation associated with the spatial variation of C pools between plots was higher than measurement errors within plots. From this study it is concluded that estimates of aboveground biomass largely underestimate total carbon stocks in forest ecosystems. Additionally, it is suggested that heterogeneous landscapes impose additional challenges for their study such as sampling intensity.
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1. Introduction

Estimates of carbon stocks in tropical ecosystems are of high relevance for understanding the global C cycle, the formulation and evaluation of global initiatives to reduce global warming, and the management of ecosystems for C sequestration purposes. However, detailed knowledge about the absolute and relative distribution of C stocks in tropical forests is still limited (Clark, 2004; Houghton, 2005).

Estimating carbon stocks and their distribution in different ecosystem pools is important to understand the degree to which C is allocated to labile and stable components. This information is also useful to estimate the amount of C that is potentially emitted to the atmosphere due to land use changes as well as from natural or human-caused fire events. In the tropics, estimates of C stocks using ground-based measurements are usually focused on quantifying the aboveground component (Houghton, 2005), while other carbon pools such as belowground biomass, necromass, and soil carbon are seldom measured. Detailed quantifications of total C stocks in tropical areas are scarce, a major cause of uncertainty associated with the assessment of this region's C balance (Schimel et al., 2001; Clark, 2004; Houghton, 2005).

Although estimations of forest biomass are abundant in the tropics, it can be inferred from Houghton et al. (2001) that there

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are several problems in published estimates of C stocks from ground-based measurements: (1) uncertainty associated with spatial variability, (2) lack of distinction between primary and secondary forests, (3) small inventory areas (<1 ha), (4) incomplete measurements of all C pools, (5) biased sample designs, (6) inadequate use of regression equations, and (7) lack of continuity in surveys.

Secondary forests are also an important component of land cover area in the tropics and for this reason they play an important role in the carbon balance of this region (Brown and Lugo, 1990). According to FAO, in 1990 secondary forests accounted for 335 million ha in Latin America (Smith et al., 1997). In Colombia, secondary forests are an important fraction of total forested area and their distribution is highly heterogeneous, mixed with croplands, grasslands, and primary forests (Etter and van Wyngaarden, 2000).

The methodological issues mentioned above, in conjunction with spatial variation of biophysical variables over landscapes, are important sources of variation and uncertainty in the estimation of carbon stocks in forested ecosystems. An average value of C stocks for an ecosystem might not be the best descriptor of this variable when spatial variation and uncertainties are high. Measures of variability such as the standard error of the mean or 95% confidence intervals should be reported in addition to the average (IPCC, 2003).

In this study we present a detailed estimation of C stocks in a tropical premontane landscape composed of a mixture of primary and secondary forests that addresses the methodological issues mentioned above. The first objective of this study was to quantify the absolute and relative quantities of C stored in different ecosystem pools and the degree of uncertainty in these estimates. The second objective was to compare the relative C stocks between primary and secondary forests for the different carbon pools to assess the effects of land use change.

2. Methods

2.1. Study site

This study was carried out in the Porce Region, Colombia ($6°45'37''$N, $75°06'28''$W) at the area locally known as Porce II where a dam was constructed in 2000 for hydropower generation. Mean annual precipitation between 1990 and 2003 was 2078 ± 601 mm ($\pm$S.D.). Precipitation is relatively homogeneous during the year with a short dry season (<15 mm per month) between December and January. Mean annual temperature at 975 m a.s.l. is 22.7 °C, with a monthly minimum of 21.3 °C and a maximum of 24.1 °C. Altitude ranges from 900 to 1500 m, a zone that represents the transition from lowland to premontane moist tropical forests. Soils are derived from granitic rocks, have low fertility, and high acidity. Twenty soil series have been described in the site and grouped in two main orders: Entisol and Inceptisol. The most common soil subgroups are *Ustoxic Dystropept*, *Typic Tropaquent*, and *Typic Tropopsamment* (Jaramillo, 1989). Mean bulk density at 30 cm depth in primary forests was estimated as 1.1 Mg m^{-3} and in secondary forests as 1.3 Mg m^{-3}.

Evidence of human settlement dates from 9000 years B.P. and suggests that shifting cultivation began 2000 years B.P. (Castillo, 1998). After Hispanic colonization (~16th century), land use changed to intensive cattle ranching, mining, and agriculture in small parcels. During the 1990s, the farms were sold and the land was abandoned due to the dam project, which promoted forest succession. Today, there is a mosaic of primary and successional forests of different ages. Primary forest fragments covers nearly 694 ha and secondary forests 1462 ha. Species composition and diversity indexes of these forests were found to be very similar to other primary forests in lowland areas. The main tree species in primary forests, according to their importance value index, are: *Anacardium excelsum* (Bertero and Balb. ex Kunth), *Jacaranda copaia* (Aubl.) D. Don, *Pourouma cecropiaefolia* Mart., *Virola sebifera* Aubl., *Oenocarpus bataua* Mart., *Miconia albicans* (Sw.) Triana, *Vochysia ferruginea* Mart., *Cordia bicolor* A. DC., *Pera arborea* Mutis, and *Pseudolmedia laevigata* (Poepp. and Endl.) Rusby. Secondary forests and fallows are dominated by light-demanding tree species such as *Vismia baccifera* (L.) Triana and Planch, *Piper aduncum* L., *Myrsine guianensis* A. DC., *Jacaranda copaia*, *Psidium guajaba* L., *Miconia affinis* DC., *Erytroxylon* sp. and *Vismia ferruginea* H.B.K. (Jaramillo and Yepes, 2004).

2.2. Permanent plots

In 1999, 33 permanent plots (20 m × 50 m, 0.1 ha) were established in primary forests and 77 in secondary forests (20 m × 25 m, 0.05 ha) by random assignment on a map for a total sampling area of 7.15 ha. Sampling points were located in the field using a GPS unit. For methodological purposes, secondary forests were distinguished in the field from primary forests by the presence of legacies that suggested previous anthropogenic interventions. The presence of large stumps, unusual soil compaction or erosion, and the massive abundance of light demanding tree species are examples of the legacies considered.

All trees, lianas and palms $\geq$10 cm in D (diameter at 1.3 m for trees without irregularities) in primary-forest plots and all plants $\geq$5 cm in secondary-forest plots were measured. Moreover, plants $\geq$1 cm in D were measured in one subplot (10 m × 10 m in primary forests and 5 m × 5 m in secondary forests) within each plot. All trees that had more than 50% of their diameter inside the plot were considered as being inside the plot; however, occurred in very few cases. Diameters were measured using calipers for plants $\geq$10 cm and digital calipers for plants $10 > D \geq 1$ cm. For buttressed trees, D was measured just above the highest buttress. Trees with irregularities were measured following the protocols reported by MacDicken (1997).

In each plot, six 1 m^2 (1 m × 1 m) subplots were established to harvest all herbaceous and non-woody vegetation <1 cm in D and all standing fine litter. Herbaceous vegetation and fine litter were completely harvested from these subplots and all material transported to the laboratory for subsequent dry weight determination. Coarse woody debris (>2 cm in diameter) was

measured in one 25 m² (5 m × 5 m) subplot in primary forests, and one 10 m² (10 m × 10 m) subplot in secondary forests. The material was weighed *in situ* and a sample of at least 10% of the total fresh weight in the subplot was collected to estimate dry weights in the laboratory of Ecology and Environmental Conservation, National University of Colombia at Medellín. In the case of large downed trees, the bole volume was estimated in the field measuring length and diameters, and a cross-section was sampled to estimate the wood density of each log. Fine root biomass (≤5 mm in diameter) was sampled using soil cores (7 cm diameter, 15 cm long) down to 30 cm depth. Only 3 plots were sampled in primary forests and 10 in secondary forests due to the laborious nature of the work. Within each plot, 10 sampling points were chosen randomly to extract one core at two depth intervals. A total of 130 cores were sampled and processed to measure fine root biomass. Cores were washed through a series of soil sieves, roots were sorted from soil and organic matter, and the final residue collected and subsequently analyzed to recover very small roots (<0.5 mm diameter). A detailed description of the methods used to sample fine roots is presented in Sierra et al. (2003). In all plots, 20 soil samples were taken to 30 cm depth. These 20 samples were mixed together and a sub-sample was taken and used to estimate C content with the Walkley–Black method (Walkley and Black, 1934). Four soil cores per plot in all plots were used to estimate soil bulk density. Additionally, six plots in each forest type were randomly selected to measure soil C to 4 m depth. Soil pits of 80 cm × 120 cm × 430 cm were excavated and four soil samples per pit were taken at 5, 10, 20, 30, 50, 75, 100, 150, 200, 250, 350, and 400 cm depth. Two of these samples were used for soil C content determination and the other two for bulk density estimation. Soil C content was estimated using the dry combustion method in a C–N analyzer (Carlo Erba NC 1500). The estimates of soil carbon are presented separately for the two methods used and depths sampled. Estimates of soil carbon up to 4 m depth are used in the final calculations of Total Carbon Stocks.

The age of 52 secondary forest plots was estimated using radiocarbon methods. The mean square diameter was calculated for each of the selected plots and a tree outside the plot with approximately similar diameter was chosen for sampling. Each of the trees was harvested and a wood sample from the base of the trunk was taken for determining C¹⁴ concentrations in tissue. Samples were analyzed at the physics laboratory of Silesia Polytechnic Institute, Poland. The age of the tree was estimated using a decay curve of atmospheric C¹⁴ over time (Lara and del Valle, unpublished manuscript). The average age of the secondary forest was interpreted as the age of the tree with the average diameter.

2.3. Biomass equations

Trees, palms and lianas were harvested and measured to collect data for local biomass equations. Individuals were selected over their entire size range to avoid extrapolations in predicting biomass of large trees.

A total of 292 trees were harvested and measured in primary and secondary forests (range in D was 0.3–198.9 cm). Diameter and height (H) were measured on every tree. Total weight of foliage, branch and bole was estimated for every tree by measuring total fresh weight in the field and drying representative samples in the laboratory to determine moisture content. Biomass equations were fit for each forest type (primary and secondary), using D or H as independent variables.

To estimate the biomass of snags we reduced the estimates using the biomass equations by 30% to account for decomposition losses of the crown. The crown biomass in these forests is around 30%. This assumption might overestimate snag mass since decomposition of the bole or the presence of heart-rot are not explicitly considered.

The root system of 49 trees was excavated to estimate coarse root (≥5 mm) biomass. All the root system was excavated for all trees until a root diameter of 5 mm. Sampled coarse roots were cleaned in the field and weighed *in situ*. A sample of about 10–20% of the total weight of the root system was taken to the laboratory to determine moisture content. The range of sampled trees was 1.7–64.6 cm in D. An allometric equation was developed with these data using D as the independent variable.

To estimate palm biomass, 41 individuals were sampled and used to fit aboveground biomass equations. A biomass equation for the species *Oenocarpus bataua* was developed separately from other palm species because of its distinct growth pattern and allometry (Hallé et al., 1978). Carbon content in biomass was estimated using 82 samples from different pools and processed with a C–N analyzer.

2.4. Calculations

Total basal area was calculated for every plot in units of m² ha⁻¹ summing up the basal area of each tree at 1.3 m height (or above buttress) and extrapolating to a hectare. Mean basal area was calculated for each forest age-class averaging the estimates from each set of plots (primary and secondary).

TCS was estimated by aggregating the mean amount of carbon in different pools (total aboveground live biomass (TAGB), total necromass (TN), total belowground biomass (TBB), and soil organic carbon (SOC)):

$$\hat{\mu} = \hat{\mu}_{\text{TAGB}} + \hat{\mu}_{\text{TN}} + \hat{\mu}_{\text{TBB}} + \hat{\mu}_{\text{SOC}}. \tag{1}$$

TAGB was obtained as the sum of the amount of carbon in the aboveground carbon pools (above ground biomass of trees >1 cm in D (AB-T), aboveground biomass of *O. bataua* (AB-Ob), aboveground biomass of other palms (AB-OP), aboveground biomass of lianas (AB-L), and aboveground biomass in herbaceous and non-woody vegetation (AHNWV)):

$$\hat{\mu}_{\text{TAGB}} = (\hat{\mu}_{\text{AB-T}} + \hat{\mu}_{\text{AB-Ob}} + \hat{\mu}_{\text{AB-OP}} + \hat{\mu}_{\text{AB-L}} + \hat{\mu}_{\text{AHNWV}})C, \tag{2}$$

where C is the conversion factor from biomass to carbon. With the exception of AHNWV, all carbon pools in Eq. (2) were estimated in each sampling plot by measuring the diameter D

(cm) or the height H (m) of each individual and then applying a biomass equation (results in kg).

The second term of Eq. (1), mean total necromass ($\hat{\mu}_{TN}$), was calculated as the aggregation of fine litter (FL), coarse woody debris (CWD) and snags (SNG):

$$\hat{\mu}_{TN} = (\hat{\mu}_{FL} + \hat{\mu}_{CWD} + \hat{\mu}_{SNG})C. \tag{3}$$

The third term of Eq. (1), carbon in total belowground biomass ($\hat{\mu}_{TBB}$), is composed of the biomass of fine (FR) and coarse roots (CRB):

$$\hat{\mu}_{TBB} = (\hat{\mu}_{CRB} + \hat{\mu}_{FR})C. \tag{4}$$

The estimation of the last term in Eq. (1), soil organic carbon ($\hat{\mu}_{SOC}$), was obtained by combining the data of bulk density and %carbon content in soil. A regression model that predicts soil organic carbon at depth was developed. Using mathematical integration of the regression equation, an estimate of soil carbon to 4 m depth was computed. A detailed description of the methods to estimate soil carbon is reported by Moreno (2004).

2.5. Statistical analysis

Biomass equations were fit to the data using linear and non-linear regression techniques. To avoid systematic bias in the utilization of the back-transformed logarithmic equations, a correction factor was used (Heien, 1968). The correction factor applied equals half the mean square error from the regression (MSE/2) and was added to the independent term of the equation.

A Monte Carlo analysis was performed to calculate the uncertainty around the final estimate of mean total carbon stocks (TCS). Total uncertainty was estimated in two separate components: the uncertainty of each pool within plots due to measurement errors (S_{within}) and the spatial variation among plots ($S_{between}$). S_{within} was calculated as the averaged variation between sub-plots within plots. For pools that were estimated using biomass equations, S_{within} was calculated as: $\hat{\sigma}_A = B\sqrt{\exp(MSE) - 1}$, with B as the estimate of the average biomass for any pool, and MSE the mean square error from the biomass equation. The spatial variation ($S_{between}$) was calculated as the standard error of the mean biomass among plots. Total uncertainty (S_{total}) was estimated as the sum of the within and between uncertainty for every pool ($S_{total}^2 = S_{within}^2 + S_{between}^2$).

Using the estimated uncertainty of each carbon pool and assuming normal distributions for the averages, a Monte Carlo procedure was used to estimate the uncertainty of the final estimates of TAGB, TN, TBB, and TCS. Random numbers were sampled from the distribution of each C pool and then summed up to produce an estimate of the aggregated pool. The procedure was repeated 10,000 times and a sensitivity analysis was performed to test the effect of correlation between variables at values of the correlation coefficient of 0, 50, and 100%. The standard deviation of the distribution of the averages (i.e. the standard error of the mean) was used as an estimate of the uncertainty of each aggregated pool. Upper and lower 95% confidence limits for the average of aggregated pools and TCS

were calculated by multiplying these standard deviations by 1.96 (*t*-value at $p = 0.975$ for ∞ degrees of freedom). Monte Carlo simulations were run in R 1.8.0 for Windows (Ihaka and Gentleman, 1996).

3. Results

3.1. Basal area

We found important structural variability in both forest types as well as a significant difference between them (Fig. 1). Mean basal area in primary forests was 36.85 ± 10.93 m^2 ha^{-1} ($\pm$S.D.), and 12.92 ± 7.71 m^2 ha^{-1} in secondary forests. Mean basal area was significantly different between both forest types (*p*-value < 0.0001, from a two sample *t*-test). Three plots showed a high basal area in primary forests. These plots were established (as the result of randomness) in sites in which large trees of the species *Anacardium excelsum* were clustered. Variability within each forest type suggests a high degree of spatial variation in the structural characteristics of these forests (Fig. 1).

3.2. Biomass equations

Tree diameter satisfactorily explained the variation in individual tree biomass for aboveground and belowground pools with the exception of palms, for which height was the best explanatory variable (Table 1, Fig. 2). All measured trees were in the range of D or H sampled for the aboveground biomass equations. Coarse root biomass was extrapolated for 23 trees (out of 11,323) that fell outside the range of tree sizes sampled to fit the equations.

3.3. Uncertainty analysis

Aboveground biomass of trees was the largest biomass pool and had the highest uncertainty, for both primary and secondary forests (Table 2). The high uncertainty is mainly explained by
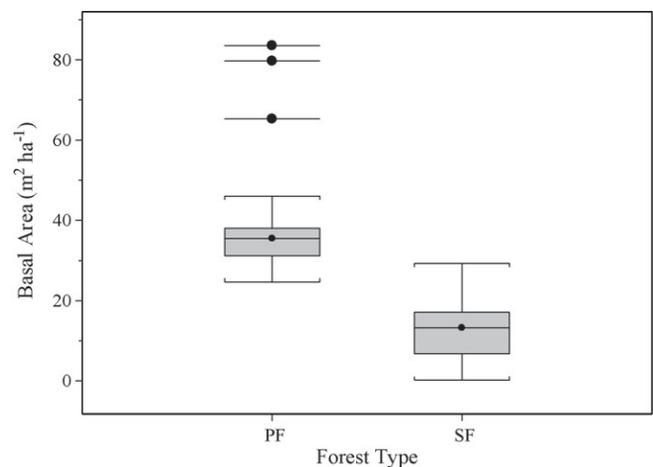
Fig. 1. Basal area estimated in primary (PF) and secondary forests (SF) plots. Boxes contain values between the 25 and 75 percentiles. Points outside the boxes represent extremely low or high observations.

Table 1
Biomass equations estimated for different pools (n = number of individuals used to fit the equation, CF: correction factor for the allometric models; R^2: coefficient of determination)

Carbon pool	Equation	Range in D or H (cm)	n	CF	R^2 (%)
Aboveground tree biomass in primary forests ($D \geq 1$ cm)	ln (AB-T) = −2.286 + 2.471 ln (D)	0.5–198	140	0.091	97.90
Aboveground tree biomass in secondary forests ($D \geq 1$ cm)	ln (AB-T) = −2.232 + 2.422 ln (D)	0.9–40	152	0.083	97.47
Coarse root biomass (primary and secondary forest)	ln (CRB) = −4.394 + 2.693 ln (D)	1.7–64.6	49	0.316	91.79
Aboveground biomass for Oenocarpus bataua	AB-Ob = 139.48 + 7.308$H^{1.133}$	50–250	83	NA	82.95
Aboveground biomass for other palms	ln (AB-OP) = 0.360 + 1.218 ln (H)	100–150	37	0.325	65.28
Aboveground biomass for lianas	ln (AB-L) = 0.028 + 1.841 ln (D)	1–11	33	0.133	87.44

The range in D or H of the individuals harvested for each equation is also shown.

the variation of AB-T estimates between plots. In general, this pattern ($S_{within} < S_{between}$) was found for the majority of the biomass pools, suggesting that the spatial variation of biomass among plots tends to be higher than the uncertainty in measuring each pool within each plot. In general, the uncertainty range for primary forests was higher than the uncertainty range in secondary forests. In primary forests the uncertainty of TCS in relative terms was 11% while in secondary forests this uncertainty was only 5%.

Our estimates of uncertainty in C stocks were sensitive to the assumption of correlation between variables (Table 3). The highest variability was obtained when a correlation of 100% between all variables was assumed. Assuming randomness between variables the total variation of TCS is reduced in 7%. Although the maximum and minimum uncertainty ranges provided in Table 3 correspond to unrealistic scenarios of correlation between variables they provide limits to constrain

our uncertainty estimates. We chose a scenario of 50% correlation to report our uncertainty ranges.

3.4. Biomass estimations

In primary forests, total aboveground biomass was estimated as 247.8 ± 40.5 Mg ha^{-1} and in secondary forests this estimate was 46.4 ± 4.3 Mg ha^{-1} (Table 4). The main fraction of aboveground biomass (92–95%) was composed by trees >1 cm in D in both forest age-classes. Palm biomass represented a minor fraction (6%) of total aboveground biomass in primary forests and was a very small fraction (0.6%) in secondary forests as well; however, palm biomass in primary forests was considerable higher (Table 4). Estimated TAGB in primary forests was about five times greater than in secondary forests. From the total mass (TM) of both forest types, which is composed by the sum of aboveground biomass, belowground
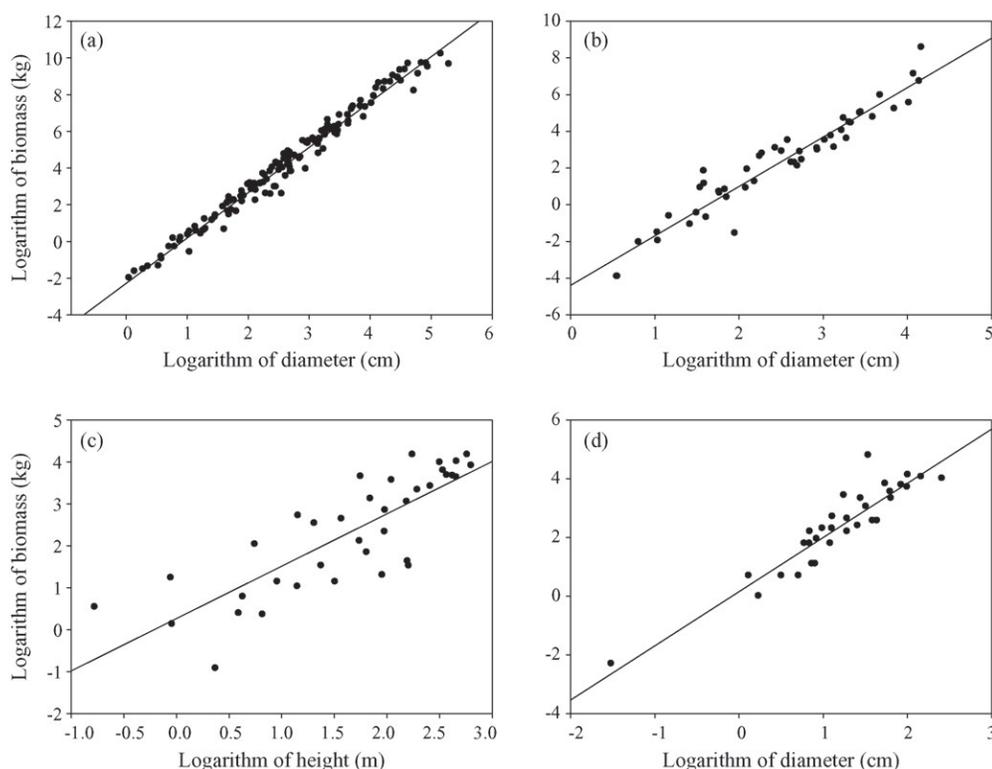

Fig. 2. Sampled data and allometric relationships between biomass and diameter or height for: (a) aboveground tree biomass in primary forests; (b) coarse root biomass; (c) other palms; (d) lianas.

Table 2
Estimates of uncertainty for each pool

Pool	S_{within}	$S_{between}$	S_{total}	n	S.E.	$\hat{\mu}$
Primary forests						
AB-T	104.19	190.50	217.13	33	37.80	228.90
AB-Ob	3.12	14.93	15.25	33	2.66	8.93
AB-OP	5.57	7.90	9.67	33	1.68	5.82
AB-L	1.95	3.29	3.82	33	0.67	3.48
AHNWV	0.74	0.22	0.78	33	0.14	0.65
FL	2.44	0.78	2.56	33	0.45	6.03
CWD[a]	NA	NA	7.25	33	1.26	6.07
SNG	3.23	4.01	5.15	33	0.90	2.67
CRB	63.89	68.93	93.99	33	16.36	67.07
FR	3.45	2.89	4.50	3	2.60	17.38
Secondary forests						
AB-T	18.76	29.00	34.54	77	3.94	43.91
AB-OP	0.32	2.85	2.87	77	0.33	0.33
AB-L	0.74	2.22	2.34	77	0.27	1.33
AHNWV	1.05	0.41	1.13	75	0.13	0.92
FL	2.03	1.91	2.79	75	0.32	4.88
CWD[a]	NA	NA	4.21	77	0.48	2.02
SNG	0.49	0.93	1.06	77	0.12	0.41
CRB	9.36	7.22	11.82	77	1.35	9.94
FR	4.55	4.78	6.60	10	2.09	15.54

Total variation (S_{total}) was partitioned between within (S_{within}) and between ($S_{between}$) variation. n: number of sampling units; S.E.: standard error of the mean; $\hat{\mu}$: estimate of mean biomass for each pool. Units in Mg ha^{-1}. AB-T: aboveground biomass of trees; AB-Ob: aboveground biomass of *Oenocarpus bataua*; AB-L: aboveground biomass of lianas; AHNWV: aboveground biomass of herbaceous and non-woody vegetation; FL: fine litter; CWD: coarse woody debris; SNG: snags; CRB: coarse root biomass; FR: fine roots.

[a] Variation cannot be partitioned because there were not replications within plots.

Table 3
Sensitivity analysis of the correlation between variables on estimates of uncertainty (coefficient of variation, %) for total above ground biomass (TAGB), total necromass (TN), total belowground biomass (TBB), and total carbon stocks (TCS)

Correlation coefficient	CV (%)			
	TAGB	TN	TBB	TCS
0	15.37	11.1	19.73	11.04
0.5	16.37	14.82	21.17	14.46
1	17.36	18.01	23.07	17.47

biomass, and aboveground necromass, TAGB represented 71.6 and 58.6% in primary and secondary forests, respectively (Table 5). Total mass in primary forests was estimated as 346.2 ± 52.8 and 79.2 ± 6.8 Mg ha^{-1} in secondary forests, and thus it was about four-fold larger than the later.

Total belowground biomass (TBB) was higher in primary forests than in secondary forests (Table 5). In primary forests TBB was estimated as 83.7 ± 17.2 Mg ha^{-1}, dominated by coarse root biomass (80% of this amount). In contrast, secondary forest TBB was estimated as 25.5 ± 3.0 Mg ha^{-1}, with fine roots representing an important fraction of this pool (60.8%). TBB represented 24.2 and 32.2% of TM in primary and secondary forests, respectively.

Total aboveground necromass (TN) was 14.7 ± 2.2 Mg ha^{-1} in primary forests and 7.3 ± 0.8 Mg ha^{-1} in secondary forests. Although TN was higher in primary forests it represented a higher fraction of total mass in secondary forests (9.2%) than in primary forests (4.2%). Most of the necromass in secondary forests is composed of fine litter (67%).

Table 4
Estimates of aboveground biomass for different pools in primary and secondary forests

	Primary forests		Secondary forests	
	Mean biomass (Mg ha^{-1}) ± S.D.	Percentage of TAGB	Mean biomass (Mg ha^{-1}) ± S.D.	Percentage of TAGB
Trees > 1 cm	228.9 ± 37.8	92.4	43.9 ± 3.94	94.6
Palms (*O. bataua*)	8.9 ± 2.7	3.6	0	0
Other palms	5.8 ± 1.7	2.3	0.3 ± 0.3	0.6
Lianas	3.5 ± 0.7	1.4	1.3 ± 0.3	2.8
Herbaceous vegetation	0.6 ± 0.1	0.3	0.9 ± 0.1	1.9
Total aboveground biomass (TAGB)	247.8 ± 40.5	100	46.4 ± 4.3	100

Table 5
Estimates of biomass pools for primary and secondary forests

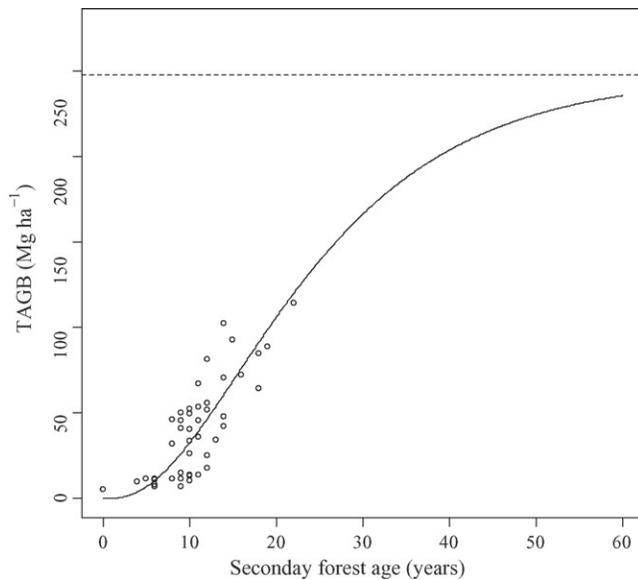|	Primary forests		Secondary forests	
	Mean mass ± S.D. (Mg ha^{-1})	Percentage of total mass	Mean mass ± S.D. (Mg ha^{-1})	Percentage of total mass
TAGB	247.8 ± 40.5	71.6	46.4 ± 4.3	58.6
Fine litter	6.0 ± 0.4	1.7	4.9 ± 0.3	6.2
CWD	6.1 ± 1.3	1.8	2.0 ± 0.5	2.5
Snags	2.7 ± 0.9	0.8	0.4 ± 0.1	0.5
TN	14.7 ± 2.2	4.2	7.3 ± 0.8	9.2
Coarse roots	67.1 ± 16.4	19.4	9.9 ± 1.3	12.5
Fine roots	17.4 ± 2.6	4.8	15.5 ± 2.1	19.6
TBB	83.7 ± 17.2	24.2	25.5 ± 3.0	32.2
TM	346.2 ± 52.8	100	79.2 ± 6.8	100

Fig. 3. Total aboveground biomass (TAGB) of 52 secondary forest plots at different ages. Radiocarbon methods were used to estimate ages in these plots (see text). The continuous line represents the best-fit model to the data: TAGB = 247 $(1 - \exp(-0.068 \times \text{age}))^{2.886}$. The discontinuous line represents the average TAGB in primary forests.

The range of ages from a set of 52 secondary forest plots (4–22 years) indicates that aboveground biomass is recovering from previous disturbance (Fig. 3). The mean age suggests that secondary forests are in an intermediate range of biomass accumulation, and will continue accumulating biomass until it approaches the current average of aboveground biomass in primary forests.

3.5. Soil organic carbon (SOC)

Organic C concentrations in soils in the first 30 cm were estimated as 29.8 ± 0.73 mg g^{-1} for primary forests and 23.4 ± 0.6 mg g^{-1} for secondary forests. Evidence for a reduction of organic carbon concentrations in secondary forests was observed (p-value < 0.05 from a two-sample comparison) compared to primary forests. Using a correction factor for the differences in bulk density between forest age-classes, the estimated SOC to 30 cm depth was 96.60 ± 2.47 Mg ha^{-1} in primary forests and 72.18 ± 2.54 Mg ha^{-1} in secondary forests (Table 6).

Estimated SOC to 4 m depth was 227.9 ± 38.1 Mg C ha^{-1} in primary forests and 192.5 ± 11.0 Mg C ha^{-1} in secondary

forests (Table 6). Estimated SOC to 30 cm represented 42% of the SOC to 4 m in primary forests and 37% in secondary forests. The estimated SOC to 1 m depth in primary forests was 70% the amount to 4 m, and in secondary forests it was 80%.

3.6. Total C stocks

Mean C content in biomass (C) was $45 \pm 1\%$. This value was used to estimate C densities in above- and below-ground biomass and necromass. In primary forests, mean TCS was 383.7 ± 55.5 Mg C ha^{-1} and was mainly composed by SOC (59%). In secondary forests, mean TCS was 228.2 ± 13.1 Mg C ha^{-1} and SOC represented 84% of this amount (Table 6).

Ratios between carbon pools were calculated (Table 7). These ratios represent C fractions between pools and can be used to estimate the proportion of C stored in different ecosystem pools (e.g. the TBB:TAGB ratio is analogous to the widely know root:shoot ratio at the ecosystem level). In primary forests C stored in TAGB was 29% of TCS, while in secondary forests it was only 9% (Table 6). Carbon in TBB was equivalent to 55% of the C in TAGB in secondary forests and 34% in primary forests. However, C in TBB was only 10% of TCS in primary forests and 5% in secondary forests. Carbon in total live biomass (TLB = TAGB + TBB) was a higher percentage of TCS in primary forests (39%) than in secondary forests (14%). Carbon in TN was 6% and 16% of the C in TAGB for primary

Table 7
Ecosystem C pool ratios in primary and secondary forests

	Numerator					
	TAGB	TN	TBB	TLB	SOC	TCS
Denominator						
Primary forests						
TAGB	1.00	0.06	0.34	1.34	2.04	3.44
TN	16.83	1.00	5.66	22.49	34.38	57.87
TBB	2.97	0.18	1.00	3.97	6.07	10.22
TLB	0.75	0.04	0.25	1.00	1.53	2.57
SOC	0.49	0.03	0.16	0.65	1.00	1.68
TCS	0.29	0.02	0.10	0.39	0.59	1.00
Secondary forests						
TAGB	1.00	0.16	0.55	1.55	9.21	10.92
TN	6.33	1.00	3.48	9.82	58.33	69.15
TBB	1.82	0.29	1.00	2.82	16.74	19.84
TLB	0.65	0.10	0.35	1.00	5.94	7.04
SOC	0.11	0.02	0.06	0.17	1.00	1.19
TCS	0.09	0.01	0.05	0.14	0.84	1.00

Table 6
Estimates of total C for different pools in primary and secondary forests

	Primary forests		Secondary forests	
	C stock (Mg C ha^{-1})	% of TCS	C stock (Mg C ha^{-1})	% of TCS
TAGB	111.6 ± 18.5	29.1	20.9 ± 2.0	9.1
TN	6.6 ± 1.0	1.7	3.3 ± 0.4	1.4
TBB	37.6 ± 7.8	9.8	11.5 ± 1.4	5.0
SOC (0–30 cm)	96.6 ± 2.5	25.2	72.2 ± 2.5	31.6
SOC (0–4 m)	227.9 ± 38.1	59.4	192.5 ± 11.0	84.4
TCS	383.7 ± 55.5	100	228.2 ± 13.1	100

and secondary forests, respectively; but its contribution to TCS is negligible (between 1 and 2% in both forest types).

4. Discussion

4.1. Plot size and spatial variability

Typically, C-stock studies are conducted within a single forest type to reduce the variation associated with spatial heterogeneity. Large sampling plots (>0.25 ha as proposed by Clark and Clark, 2000) are used to minimize the variation within the forest type. The notion of homogeneous space (Turner and Chapin, 2005) is implicit in those studies. Using a modeling exercise, Smithwick et al. (2003) have shown that the homogeneous approach in the study of C dynamics for a heterogeneous landscape could lead to erroneous representations of broad-scale processes. To capture these small-scale processes a large sample size is helpful. A large number of sampling plots is also useful to assess the spatial variation of C stores when the landscape is a mosaic of forests with different ages, disturbance regimes, and legacies.

In terms of C stocks the study site is a spatially complex landscape because it comprises a large number of patches of different land use history, soil, slope, and donor ecosystems for regenerating secondary forests. The interaction of these factors produces a high variation in forest cover within the landscape.

In this study we preferred to establish a large number of small plots instead of the classical establishment of a large single sampling unit due to the landscape complexities mentioned above. A large number of plots allows the estimation of spatial variability of carbon stocks, which increases the confidence in the C estimates (i.e. a large number of samples
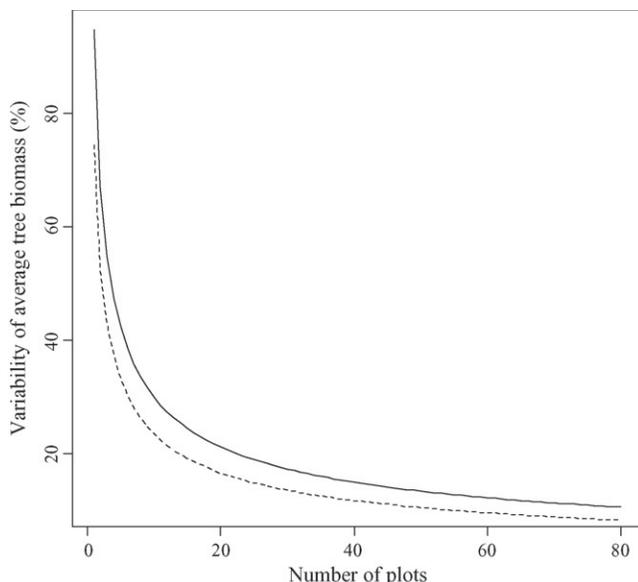

Fig. 4. Effect of increasing number of plots on the variation in the estimate of mean aboveground tree biomass in primary (continuous line, 0.1 ha plots) and secondary forests (discontinuous line, 0.05 ha plots). Variability is reported as the proportion of standard error and mean aboveground tree biomass expressed as a percent. Standard errors calculated as the proportion of standard deviation and the number of plots for a given point.

reduces the standard error of the mean). The coefficient of variation of the estimates of aboveground tree biomass shows that at least 20 plots of 0.1 ha are required to obtain a standard error of the mean less than 20% relative to the average (Fig. 4). This result contrasts with those of Nascimento and Laurance (2002) who found that three plots of 1 ha can provide a precise estimate of aboveground biomass in Amazonian forests. This contradiction may be explained by the fact that Amazon forests tend to be fairly homogenous over the landscape whereas premontane forests in the Andes are patchy and heterogeneous (Etter and van Wyngaarden, 2000; Armenteras et al., 2003). With three sampling plots it would not be possible to sample the actual level of variation over the latter landscape. This difference in opinions of the appropriate plot size and number at the landscape level can be influenced by the size of the plots and whether within-plot variability is reported. A small number of large sampling plots may have a smaller between-plot variance than a similar number of smaller plots as long as the grain size of variability is smaller than the large plots. However, if this is true then the reduction in between plot variance is likely to come at the expense of increasing within-plot variance.

4.2. Importance of including an uncertainty analysis

Uncertainty analyses help to identify the major drivers of variation of C pools in forest ecosystems (Chave et al., 2004). Our analysis showed that the error associated with measuring C pools in these forests was usually lower than the variation of the pools themselves across the landscape. This study also shows that a large number of sampling plots reduces the uncertainty in the final estimates. Further study designs for carbon inventories in heterogeneous landscapes should focus on obtaining more replicates of the sampling unit rather than the extent of the unit itself. Here we found that the variation of the larger pools such as soil carbon is the main source of the variation in the final estimate of aggregated pools. This indicates that more effort should be directed in the sampling intensity and accuracy of large pools.

Soil carbon was the largest C pool in the ecosystems studied; however, our estimate has high uncertainty, mainly due to the size of this pool and the small number of samples used to estimate SOC to 4 m depth (six plots per forest type). Because of this uncertainty, significant differences were not found in SOC to 4 m depth between primary and secondary forests (p-value = 0.156, from a t-test).

Total carbon stocks in primary forests are more variable than in secondary forests. In primary forests a 95% confidence interval for mean TCS was estimated as 299.4–467.9 Mg C ha^{-1}, while for secondary forests this interval is only 206.0–250.4 Mg C ha^{-1}. Although most of this variation is explained by the uncertainty in the estimation of SOC, it is interesting that the variation of the estimates of AB-T was very similar between primary and secondary forests (Fig. 4). In secondary forests a number of factors may be associated with this variation, previous land use and age being the most important. Similarly, natural disturbances in primary forests

seem to play an equivalent role in terms of the variation of C stocks.

4.3. Comparison to other regions

Although the primary forests studied here are located in the premontane moist life zone (*sensu* Holdridge), our estimation of aboveground biomass is in the range of other estimates in moist and wet lowland tropical forests. The confidence interval obtained here for the average TAGB in primary forests (207.3, 322.7 Mg ha^{-1}) is consistent with other estimates of TAGB in tropical sites. The estimated mean TAGB for primary forests in this study was similar to those found in old-growth lowland moist forests in Barro Colorado Island, Panama (214.4 ± 46.4 Mg ha^{-1}) and La Selva, Costa Rica (234.0 ± 60.9 Mg ha^{-1}) (DeWalt and Chave, 2004), even though these estimates are biased to locations of tall forests without gaps. Laurance et al. (1997) found that biomass tends to decline in forest edges as an effect of fragmentation. The primary forest fragments in our study area indicate that even after the dramatic effects of fragmentation these forest remnants can still store large amounts of carbon. Our estimate is also in the range of estimates of aboveground live biomass for the Amazon (Houghton et al., 2001). These results suggest that changes in altitude, at least up to 1500 m a.s.l., do not play an important role in determining TAGB in tropical forests. Instead, precipitation and anthropogenic interventions may be more important factors explaining stores of TAGB.

Our estimate of *TBB* is among the largest values reported in the literature for tropical forests (Sanford and Cuevas, 1996; Cairns et al., 1997; Jackson et al., 1997), which can be explained by three different factors. First, many studies of belowground biomass in the tropics only measure one component of the total belowground pool. In this study we measured fine and coarse roots with two different methods to account for the largest amount of biomass possible. Second, belowground biomass studies in montane forests generally show higher biomass values than in lowland forests (Sanford and Cuevas, 1996). Given that our study site is located between lowland and montane forests it is likely that our estimate of TBB will be in an intermediate range of previously reported studies. Averages for montane and lowland tropical forests have been reported as 125 and 32 Mg ha^{-1}, respectively (Sanford and Cuevas, 1996). Our estimates of TBB were 83.7 and 25.5 Mg ha^{-1} for primary and secondary forests, respectively. Third, our estimates for fine roots include both live and dead biomass. Although we do not know the proportion between live and dead fine roots it is possible that dead fine roots account for a large proportion of the total fine root mass. For this reason, our estimates of TBB have to be interpreted carefully.

4.4. Relative importance and stability of pools

In our area, lianas play a more important role in secondary than in primary forests. Conversely, palms are more prominent in primary forests (Table 4). This pattern suggests a change in forest composition, probably due to changes in light availability

as succession proceeds to older stages. However, this change in community structure is not associated with important changes in the relative distribution of aboveground biomass. Trees >1 cm in diameter represent more than 90% of TAGB in both forest types, which highlights the relevance of quantifying this C pool in tropical forest ecosystems.

TAGB is the most sensitive of all pools to anthropogenic interventions. In primary forests TAGB is five times higher than in secondary forests, while TBB and TN are only three and two times higher, respectively.

Although the difference of SOC to 4 m depth between the two forest types was not significant, the net difference between the two forest types was 35.4 Mg C ha^{-1}. At 30 cm depth, where the sample size was higher and land use changes are more pronounced, the difference between the two forest types was significant (*p*-value < 0.05 from a *t*-test). For the other C pools (TAGB, TBB, and TN) differences between primary and secondary forests are enormous due to the anthropogenic disturbances. These data show that soils are more resistant than any other pool to C losses associated with human perturbations.

Following deforestation these forests were used for cattle pastures and as a result some soil properties such as structure were degraded. This disturbance is probably also associated with the observed increase in the TBB:TAGB ratio from primary to secondary forests. Here we hypothesize that different resource limitations between the two forest age-classes are responsible for a shift in C allocation from aboveground to belowground plant parts when primary forests are converted to secondary forests. The high contribution of fine root biomass to TM in secondary forests suggests that belowground limitations are higher in this forest type than in primary forests (Chapin et al., 2002). Increased light competition as succession advances probably plays a more important role in the allocation of C to aboveground plant parts in primary forests.

4.5. Effects of land use

For the entire area of study (2156.5 ha) the 95% confidence interval of carbon stored in the ecosystems is between 509.1 and 690.8 Gg with a mean of 601.0 ± 34.0 Gg C. If these forests were not deforested previously they would store between 650.0 and 1009.9 Gg C, which is on average 38% more carbon than what is currently stored in the area.

Given our results, the deforestation of 1 ha of primary forests in the Porce region would cause the emission of about 155.8 ± 19.0 Mg C to the atmosphere. The deforestation of all the remaining primary forests of this region would cause the emission of 108.4 ± 13.1 Gg C. We estimate that the amount of carbon emitted to the atmosphere in this region at the time of forest to pasture or agriculture conversion was between 174.0 and 283.2 Gg C.

Since secondary forests cover a larger area (67.8% of the total area) than primary forests (32.2%), the total amount of carbon stored in secondary forests (333.7 Gg) was higher than in primary forests (266.2 Gg). However, in terms of the relative contribution of each forest type to TCS in the landscape, primary forests contained nearly the same proportion as secondary forests

(44.4 and 55.6%, respectively). This means that about a half of the carbon in the landscape is stored on a third of the land.

Assuming that primary forests are in a C balance we believe that the total area is acting as a carbon sink because secondary forest is the dominant forest type in this landscape. These regrowing forests are recovering from previous disturbances and their current biomass accumulation trend shows that they will keep accumulating biomass at least for the next 20 years (Fig. 3). However, if the decline in forest edges as an effect of fragmentation is similarly to the degree it has been reported previously (Laurance et al., 1997; Nascimento and Laurance, 2004), then it is possible the primary forest remnants are a source and the overall landscape is less of sink than indicated from the secondary forests alone. This hypothesis only could be tested by monitoring changes in C stocks and fluxes over time.

It is important to note that the pattern of land use change in this region was driven directly by the construction of the hydroelectric dam and it is not representative of other land use change processes more common in the Andes or the Amazon (e.g. Fearnside, 1996). The transformation of agricultural lands to the secondary forests assessed in this study was the result of local environmental laws that mandated the mitigation of negative environmental effects after the construction of a dam. Adjacent areas to the landscape studied here did not follow the land use changes documented in our study.

Homogenous areas of tropical forests are decreasing with secondary and primary forest fragments playing an increasing role in the composition of tropical landscapes. This study shows that heterogeneous landscapes can store important quantities of carbon but impose additional challenges for their study such as sampling intensity. Efforts to study the global C balance, especially in the tropics, should acknowledge the increasing role of heterogeneous landscapes due to anthropogenic perturbations and natural variability. A landscape approach to studying the C balance and the biogeochemistry of tropical forests would improve our ability to address global questions about elemental cycles.

Acknowledgements

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