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Secondary Vegetation in Central Amazonia: Land-use History Effects on Aboveground Biomass

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ABSTRACT

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Growth of secondary forest (*capoeira*) is an important factor in absorption of carbon from the atmosphere. Estimates of this absorption vary greatly, in large part due to the effect of different land-use histories on the estimates available in the literature. We relate land-use history to aboveground biomass accumulation of secondary vegetation in plots on land that had been used for agriculture (unmechanized manioc and maize) and for pasture in small rural properties in the Tarumã-Mirim settlement near Manaus in central Amazonia, Brazil. We evaluated influence of a) age of the second growth vegetation, b) time of use as agriculture or pasture and c) number of times the area was burned. Biomass data were obtained by destructive sampling of all plants with diameter at breast height > 1 cm in 24 parcels of secondary vegetation ranging from 1 to 15 years of age in abandoned pasture (n = 9) and agriculture (n = 15). As compared to secondary vegetation in abandoned agricultural fields, vegetation in abandoned cattle pasture (the predominant use history for Amazonian secondary vegetation) grows 38% more slowly to age 6 years. Number of burns also negatively affects biomass recovery. Applying the growth rates we measured to the secondary forests reported in Brazil's Second National Communication to the United Nations Framework Convention on Climate Change suggests that carbon uptake by this vegetation is overestimated by a factor of four in the report.

KEYWORDS

Amazon, Biomass; Brazil; Global warming; Land use; Secondary vegetation

1. Introduction

The growth rates of secondary forest represent important inputs for calculating net emissions of greenhouse gases from land-use change (e.g., Fearnside, 1996, 1997, 2000) and for the productivity and sustainability of agriculture that depends on fallow periods between periods of cultivation (e.g., Silva-Forsberg and Fearnside, 1997). Secondary vegetation growth has a significant role in national accounts of greenhouse-gas emissions, but uncertainty in these accounts is very high. Brazil`s first inventory under the United Nations Framework Convention on Climate Change claimed that secondary vegetation in the country's Amazonia biome was absorbing 34.9×10^6 Mg C year^{-1} over the 1988 - 1994 period (Brazil, MCT, 2004, p. 147). Information presented in the second inventory indicates an absorption of 9.0×10^6 Mg C year^{-1} for 1994 - 2002, the reduction being due to a smaller estimated area of secondary vegetation (Brazil, MCT, 2010, p. 242). Despite the magnitude of these numbers, the estimates are not based on any actual measurements of secondary-forest growth (see: Fearnside, 2013).

Brazil's Legal Amazon region, which occupies 5×10^6 km^2 or about 60% of the country, has a wide variety of different land uses replacing natural forest, each with different implications for secondary-forest growth. Mechanized agriculture, primarily for soybeans, is almost all located along the southern edge of the region, especially in the state of Mato Grosso (Fearnside, 2001). Cattle pasture is the predominant land use in the remainder of the region, including the Manaus area in central Amazonia. Pasture is planted both by actors of all sizes: large (defined in Brazil as > 1000 ha) and medium (101-1000 ha) ranchers and by small (≤ 100 ha) farmers (Fearnside, 2005, 2008). Large and medium landholders have long been the main agents of deforestation and pasture planting in Brazilian Amazonia (e.g., Fearnside, 1994). However, a comparison of data from 2002 and 2009 indicates a marked decrease in the average size of clearings (Rosa et al., 2012) and an increase in relative terms in the role of small farmers. The large overall decrease in Brazil's deforestation rate that began in 2005 was disproportionately among larger actors, especially since 2008 (Godar et al., 2014). The number of small farmers has steadily increased, as has the number of government-sponsored settlement projects; by 2013 they totaled 3325 projects. Considering the 2738 of these for which data are available, deforestation in the projects totaled 161,833 km^2 through 2013, or 21% of the total by that year in Brazil's Legal Amazon region (Yanai et al., 2015).

Large ranchers almost always plant pasture directly after clearing the forest, while small farmers often plant annual crops such as manioc and maize for several years before the area is converted to pasture. These farms may have areas under fallow between use periods under annual crops. This is similar to swidden or shifting cultivation, such as that practiced by indigenous and other traditional peoples whose cultural traditions include use of fallows as part of a cycle that can sustain production indefinitely (e.g., Nye and Greenland, 1960). In the case of small farms in Amazonian settlement projects, no such long-term adjustment has taken place, and cropping is most commonly supplanted by pasture after a few years, the continued planting of annual crops depending on continued advancement of clearing into the remaining forest (e.g., Fearnside, 1986). We refer to this form of agriculture as "slash-and-burn." This paper only considers secondary vegetation derived from slash-and-burn agriculture and from cattle pasture (in small-farmer lots in both cases).

In Amazonia, biomass accumulation rates of secondary vegetation (known as "*capoeira*" in Brazil) can be limited by factors related to land-use history (Buschbacher et al., 1988; Fearnside and Guimarães, 1996; Finegan, 1996; Moran et al., 2000; Steininger, 2000; Uhl, 1987; Uhl et al., 1988). Intensity of prior land use is reflected in natural regeneration and is related to: 1 – type of previous land use at the site, such as slash-and-burn agriculture, cattle pasture, tree planting or exploitation of charcoal; 2 – age of secondary vegetation (time since abandonment); 3 – time that the area remained under agriculture and ranching activity prior to abandonment; 4 – method used for removal of vegetation (preparation of the soil) such as burning versus mechanical clearing and grinding; and 5 – frequency of occurrence of disturbances such as burning and weeding.

Fearnside and Guimarães (1996) observed that secondary forests with a pasture use history accumulate less biomass than do stands established in abandoned agricultural areas in Altamira, Pará. Brazil. Pasture use also results in secondary vegetation with floristic compositions that differ from those in areas without this history, as shown by studies in the Manaus Free Trade Zone Agriculture and Ranching District (DAS) in Brazil's state of Amazonas (Longworth et al., 2014; Mesquita et al., 2001). Uhl et al. (1988) observed that secondary vegetation developed from pasture with lighter use intensity accumulated 40% more biomass than did stands of the same age, but with more intensive use history in Paragominas, Pará. Moreira (2003) noted that the number of burns negatively influences biomass inventory of natural regeneration in areas that had been used for pasture, agriculture and rubber plantations north of Manaus. Annual rate of biomass accumulation decreases with increase in age of secondary vegetation (*e.g.*, Lucas et al., 1996).

Based on data from destructive measurements in the Venezuelan Amazon, Uhl (1987) established a practical model to estimate biomass stock in secondary vegetation using time since abandonment as the only independent variable, but did not include variables related to land-use history. Zarin et al. (2005) developed models to estimate biomass with wide applicability in Amazonia, including soils with a range of sand and clay contents. In addition to the age of the secondary vegetation, these authors considered climatic data (such as temperature and the duration of the dry season), but they did not include variables related to land-use history. Silver et al. (2000) also developed model estimates for biomass in different rainfall regimes in tropical regions and for different land-use types using age as the independent variable, but not including the time the site was used and number of burns.

Stocks and accumulation rates of biomass need to be quantified in Amazonian secondary vegetation in order to better understand successional processes so that appropriate management can be proposed. Here we develop models based only on land-use history factors, making these models more practical, although less precise, than either direct measurement by destructive sampling or estimates requiring allometric data and species identifications (*e.g.*, Wandelli and Fearnside, manuscript).

Secondary-vegetation growth rates have major implications for the net emissions of carbon from land use and land-use change in Amazonia. We examine the implications of our results for the carbon uptake calculated in Brazil's national inventory of greenhouse-gas emissions reported in the country's second national communication to the United Nations Framework Convention on Climate Change.

2. Materials and methods

2.1. Study area

Our study was carried out in secondary vegetation in rural properties in the Turumã-Mirim agrarian reform project, located to the northwest of the city of Manaus, Amazonas, Brazil (Figure 1). The original forest is classified as dense *terra firme* (unflooded upland) forest (Braga, 1979) and the soil is predominantly allic yellow latosol (Oxisol) with high clay content (Brazil, IPEAAOc, 1971). The climate is Ami in the Köppen system, with mean annual rainfall around 2200 mm and a three-month dry season.

[Figure 1 here]

The Tarumã-Mirim Agrarian Reform Project was established in 1992 for 1042 families, each with a 40-ha lot. The area is described by de Matos et al. (2009) and Coelho et al. (2012). Since the area is located approximately 35 km by road from the city of Manaus (population ~2 million), it is influenced by urban markets for charcoal, manioc flour and meat.

2.2. Direct destructive assessment of biomass

Aboveground biomass (AGB) of each of 24 secondary-vegetation stands between 1 and 15 years of age was measured directly by destructive sampling, and individual plant measurements and weights were obtained with diameter at breast height (DBH) ≥ 1 cm (DBH = diameter 1.3 m above the ground) for developing allometric equations. A total of 2268 plants in 146 species were weighed and height and diameter at breast height (1.3 m above the ground) were measured. Water contents and dry weights were obtained for trunks, branches and leaves of 3-5 individuals (if present) of each species in each 100-m^2 plot. Each of 24 stands had a single plot laid out as a 10 × 10 m square randomly positioned within each stand but located at least 10 m from the edge of the secondary-vegetation stand and at least 50 m from the edge of the forest.

Information about land-use history of secondary vegetation in each lot was obtained through interviews with various members of the family that owned the lot (Table 1). This information was supplemented and validated through interviews with neighbors who could remember when the vegetation was cut and burned because they had collaborated in collective work exchanges (*mutirões*) in the lot or because they were concerned about uncontrolled fire entering their own fields. Inventories and destructive measurements of biomass were only made in secondary-vegetation stands where information about use history was consistent with our observations of remains still present in the area and where this coincided with the opinions of all informants.

[Table 1 here]

2.3. Data analysis

Data analysis used standard regression analyses (Zar, 1999). These were performed using Systat software.

2.4. Use of biomass evaluated with direct methodology to assess allometric models

We used data from our destructive sampling to assess the adequacy of the main multi-specific allometric equations used in the literature to estimate biomasses of individual trees in secondary vegetation in central Amazonia. The mean errors of the estimate (percentage error between the weight obtained directly and that estimated using the equations) for total accumulated biomass (Mg ha^{-1}) were compared. Sums of the observed dry weights and those obtained from allometric equations of all the trees in each plot were extrapolated to a one-hectare area to obtain total biomass (Mg ha^{-1}) to allow comparison at the stand level.

3. Results

3.1. Models for estimation of accumulated biomass based on land-use history

Secondary-vegetation stands with a history of use as pasture (n = 15) and as agriculture (n = 9) were analyzed separately because they showed different relations between biomass and secondary-vegetation age (Figure 2), which was the land-use history variable with greatest influence on biomass accumulation. In secondary-vegetation stands with ages between 1 and 6 years that originated from agriculture, accumulated biomass (Mg ha^{-1}) was best explained by a log-linear model (r^2 = 0.959; error of estimate = 13.5%) using age as the only independent variable, while models that included time of use and number of burns produced errors of up to 50% (Figure 3 and Table 2).

[Figures 2 & 3 + Table 2 here]

Biomass accumulated in secondary vegetation up to 15 years of age derived from abandoned pastures was not sufficiently explained by the age variable (r^2 = 0.797) and had an error of the estimate of 36% (Table 2). Variation in biomass of secondary vegetation derived from pasture was much better explained when, in addition to the age variable, regressions included total time of land use and number of burns. These three variables are correlated because, in areas of family farming, the longer the time since a given site was cleared of primary forest the longer it is likely to have been used and the greater the number times it has been burned. We therefore tested various combinations of these three factors linked to land-use history to build an index for fitting a simple regression model.

To assess the influence of time of use on biomass of secondary vegetation we isolated the age variable by dividing stand age by land-use time so as to avoid needing to use rate of accumulation per year as the dependent variable. Using this rate as the dependent variable would mask the influence of the time the land remains in use because it is a function of age. The exponential model whose independent variable was the quotient of age divided by the time of use produced a good fit for biomass accumulated in pasture areas (r^2 = 0.957; error of the estimate = 19.9%) (Figure 4 and Table 2). The error of the estimate for biomass of secondary-vegetation stands derived from pasture fell to 14.9% when number of burns was added as an independent variable in the model. The index “age of the secondary vegetation/time + number of burns” explained 97.5% of the variation in accumulated biomass (Mg ha^{-1}) in secondary-vegetation stands established in pasture areas (Figure 5 and Table 2).

[Figures 4 & 5 here]

3.2. Comparison of model results with biomass determined directly

Mean error of the estimate for accumulated biomass varied from 7.6% to 57.5% for the eight sets of models selected from the literature and from this study, as compared to data measured directly in the 24 destructive estimates (Figure 6 and Table 3). Strictly for comparative purposes, we fit the linear model that Higuchi et al. (1998) derived for a set of primary-forest species from the same central Amazon region at a site approximately 20 km away. As expected, the model for primary-forest species did not fit the data for biomass of secondary vegetation in this study (Table 3, Model 1).

[Fig. 6 & Table 3 here]

The set of equations in Model 3 derived by Uhl et al. (1988) from multispecies regressions for leaves and wood in Amazonian secondary vegetation in the state of Pará, using DBH as the independent variable, also generated a very high error of the estimate (48.7%). This was similar to the error of the estimate of 48% obtained from Model 2, which Uhl (1987) derived for the Venezuelan Amazon with age as the only independent variable. Model 6 (this study), which used land-use history as an independent variable, had a mean error of only 14%. In Model 6, age of the secondary-vegetation stand was the independent variable of the regression for biomass of secondary-vegetation areas derived from agriculture, and the index "age/time of use + number of burns" was the independent variable used to estimate biomass of secondary vegetation derived from pasture.

The detailed multi-specific regression model developed by Nelson et al. (1999) (Model 4), which was based on DBH of seven secondary-vegetation species in central Amazonia at a site located approximately 30 km from our study area (but with the difference of being a former rubber plantation that had been cleared mechanically), had a high error of the estimate (41%) for accumulated biomass using the data measured in this study. This error of the estimate for accumulated biomass was reduced to 19% when we used Model 5 (Nelson et al., 1999) in which the authors added the height variable.

Model 7 (this study) which was applied to all species, including lianas with DBH $\geq$ 1 cm, resulted in the best fit for total biomass (Mg ha^{-1}) of secondary vegetation. Mean error of the estimate was 10.2%.

The lowest mean error of the estimate for total biomass (Mg ha^{-1}) of the eight models tested was 7.6% (Model 8). For estimating biomass of lianas we applied the equation developed by Gehring et al. (2004) for lianas in both secondary vegetation and primary forest in central Amazonia. For bushy species we used our multispecies regression and for estimating biomass of all species in the genus *Cecropia*, which has low stature and a low wood density of around 0.27 g cm^{-3}, we applied our *Cecropia ulei* model (Wandelli and Fearnside, manuscript).

The relative growth rates for secondary forest derived from slash-and-burn agriculture and from pasture can be visualized from the equations in Table 2. If one considers the equations that use only age, a 6-year-old secondary vegetation stand derived from slash-and-burn agriculture has an aboveground biomass of 50.3 Mg ha^{-1} (i.e., a growth rate of 8.4 Mg ha^{-1} year^{-1}), while a stand of the same age derived from pasture has aboveground biomass of 31.1 Mg ha^{-1} (i.e., a growth rate of 5.2 Mg ha^{-1} year^{-1}). The secondary vegetation following pasture grows 38% more slowly than that following use as slash-and-burn agriculture.

4. Discussion

Our analyses point to the importance of considering land-use history in models for estimating accumulation of biomass in secondary-vegetation stands. Models that are more practical but less precise (error of the estimate = 14%) than those derived from biometric measurements of trees were developed to estimate total aboveground biomass (Mg ha^{-1}) indirectly using as independent variables the time since abandonment of agriculture or ranching activity (age of secondary vegetation in years), total time of land use under agriculture or pasture (years) and number of times that the vegetation of the area was burned. Equations for natural regeneration were developed separately for abandoned pastures and for areas of slash-and-burn agriculture because both the intercept on the ordinate and the slope of the line for data on biomass versus stand age with each of the two land-use histories were different, and areas of pastures have more negative impact on biomass accumulation in natural regeneration than areas with histories of itinerant agriculture. Stand age explained 96% of variation in biomass of areas regenerating from agricultural activities, but biomass of secondary vegetation derived from pastures was more certain (98%) when an index was used that included time of land use and number of burn (in addition to stand age). Cattle pasture produces a larger negative impact on natural regeneration than does agricultural activity (Fearnside and Guimarães, 1996; Lucas et al., 1996; Steininger, 2000; Uhl et al., 1988), and time of land use therefore becomes decisive for successional processes and accumulation of biomass in natural regeneration of abandoned pastures.

Because livestock is generally an older activity than is agriculture in the settlement project, stands derived from slash-and-burn agriculture evaluated in this study had narrower ranges the explanatory variables as compared to stands derived from pasture. In addition, influence on biomass stocks from time of use and from number of burns can be expected to be smaller in secondary vegetation from agriculture than in abandoned pastures because soil physical structure is damaged by cattle.

Note that in the present study the distance to a propagule source (remaining forest) was similar for plots with the two land-use histories. Forest was present within few hundred meters (but never < 50 m) in all of the 40-ha lots. For Brazilian Amazonia as a whole, the contrast in secondary-vegetation growth rates between slash-and-burn agriculture and pasture can be expected to be greater than our data show, since much of the pasture is in vast clearings on large ranches far from propagule sources, while slash-and-burn agriculture is typically done in smaller clearings near forest, similar to the plots we studied.

A number of studies have shown the damaging effects of pasture use. Using remote-sensing techniques, Moreira (2003) concluded that number of burns determined stocks and accumulation rates of biomass in abandoned pastures in an area in central Amazonia close to the location of the present study. Zarin et al. (2005), using data on biomass in nine Amazonian ranches, concluded that five or more burns in the same area not only reduces the accumulation of carbon by more than 50% but also slows closing of the canopy, a delay that would make the secondary vegetation more susceptible to fire. An excessive number burns, together with soil erosion, can damage the seed bank such that natural regeneration then becomes wholly dependent on immigrant species (Janzen and Vásquez-Yanes, 1988). Slower recovery of secondary vegetation in abandoned pastures as compared to agricultural fallows is a general phenomenon throughout the tropics (see review by Chazdon, 2014).

Zarin et al. (2005) developed models for estimating biomass of secondary-vegetation stands using the age of the secondary-forest stands as the independent variable. Zarin et al. (2005) developed one equation for sandy soils and another for non-sandy soils based on data on the biomasses at nine sites distributed over a large part of the Amazon region. They used direct and indirect methods, but in spite of their having included aspects related to the climate, the models did not include variables related to the history of land use, such as the type of activity, time of use and number of burns. Silver et al. (2000) developed models to estimate biomass based on a set of 143 measurements from the literature on secondary vegetation in tropical countries. These authors also used the time of abandonment of the capoeira as independent variable (including ages between 0.3 and 80 years), for each of the three rainfall regimes (<1000 mm; 1000 - 2500 mm; >2500 mm) and for each of the three uses (pasture; itinerant agriculture; and it drops and it burns of the forest without planting). However, the models of Silver et al. (2000) did not include equations that include the combination of precipitation and use history, and nor the time of use and number of times that the vegetation was burned, which were decisive variables in the models developed in this study for pastures

Biomass models based on land-use history may be useful for obtaining values that are applicable to wide areas and that do not require high precision and, moreover, due to the ease of implementation and low cost, may be used by rural communities to computed carbon credits from their secondary-vegetation stands. The destructive methodology can cost an average US$ 11 per tree for aboveground biomass or US$322 per tree if root biomass is also measured (Silva, 2007). A factor limiting applicability of these models is difficulty of obtaining precise information from farmers on the history of secondary vegetation stands and the considerable effort needed to check information with family members, day laborers and neighbors. While this interview information is the only field input needed, obtaining it is not always successful, which restricts the number of secondary-vegetation stands to which this methodology can be applied.

The growth rates of the secondary vegetation we studied indicate a substantial overestimate of carbon uptake by this vegetation in Brazil's national inventories of greenhouse-gas emissions. In Brazil's second national communication to the United Nations Framework Convention on Climate Change, the assumption was that in 2002 the biomass of secondary vegetation stands on any land that changed status from another land use to secondary forest between 1994 and 2002 would be 35% of the biomass of the "primary" vegetation characteristic of the site (Brazil, MCT, 2010, p. 239). Assuming a constant rate of conversion to secondary vegetation over the 8-year period from 1994 to 2002, the average age of this secondary vegetation in 2002 would be 4 years. The inventory considers the carbon stock in the primary vegetation at this site (forest type "Db", RADAMRASIL volume 18) to be 158.01 Mg C ha^{-1}, including 27.1% (42.8 Mg C ha^{-1}) in belowground biomass (Brazil, MCT, 2010, pp. 235-236). The aboveground carbon stock of the "primary" forest is therefore 115.2 Mg C ha^{-1}, and the presumed aboveground stock in 4-year-old secondary vegetation is 40.3 Mg C ha^{-1}, implying an accumulation rate of 10.1 Mg C ha^{-1} year^{-1}. Assuming a carbon content for secondary vegetation of 45% (e.g., Fearnside, 2000), this corresponds to a growth rate of 22.4 Mg of dry aboveground biomass per hectare per year. Calculating growth rates from our data for 4 years of growth (as was done earlier for 6 years of growth), secondary vegetation following slash-and-burn agriculture grows at 8.2 Mg ha^{-1} year^{-1} and following pasture at 5.1 Mg ha^{-1} year^{-1}. The inventory rate is therefore 2.7 times higher than our rate for regrowth after slash-and-burn agriculture and 4.4 times higher than our rate for regrowth after pasture. For secondary forests at this location that were already present in 1994 and remained so in 2002, the inventory assumes an aboveground biomass carbon accumulation rate of 4.5 Mg C ha^{-1} year^{-1} (Brazil, MCT, 2010, p. 238), equivalent to a growth rate of dry aboveground biomass of 10 Mg ha^{-1} year^{-1}, or 1.2 times higher than our rate after agriculture and 2.0 times higher than our rate after pasture. If one considers the land use transition and carbon uptake data from the inventory (Brazil, MCT, 2010, p. 242), only 8.6% of the secondary forest is derived from agriculture, versus 91.4% from pasture, assuming that the percentages that apply to the land that was under these two land uses in 1994 (86.4% of the total area that transitioned to secondary forest) also apply to the remaining 13.6%. Most (94.7%) of the inventory's absorption by secondary forests comes from transitions into this land use, the remaining 5.3% coming from secondary forests that remain as secondary forests throughout the 1994-2002 period. Given the overestimates of carbon absorption by the two types of land-use history and the two periods of origin (transitions into secondary forest within the 1994-2002 period versus entering this period as pre-existing secondary forest), the overall exaggeration of secondary vegetation carbon uptake in the inventory is by a factor of 4.1. The absolute amount of the overestimate is 6.8×10^6 Mg C year^{-1}. As an indication of the magnitude of this value, it represents 8.3% of all of Brazil's CO_2 emissions from fossil fuels in 2005 (Brazil, MCT, 2010, p. 270); for comparison, the São Paulo metropolitan area represents almost exactly 10% of Brazil's population and presumed emission.

5. Conclusions

1.) Secondary vegetation grows more slowly (by 38% to age 6 years) in abandoned cattle pasture than in plots that had been used for slash-and-burn agriculture.
2.) Secondary vegetation biomass growth is negatively related to the number of times a site has been burned.
3.) Biomass estimates that include information on land-use history (time under agriculture or pasture use and number of burns) produce more reliable estimates than do regressions based only on secondary-vegetation age.
4.) Applying our biomass accumulation rates to the carbon uptake calculated in Brazil's national inventory of greenhouse-gas emissions implies that uptake was overestimated by a factor of four.

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FIGURE LEGENDS

Figure 1 – Location of study area: the Tarumã-Mirim Agrarian Reform Project, Amazonas state, Brazil.

Figure 2 – Relationship between aboveground biomass (Mg ha^{-1}) and the age of nine secondary-vegetation (*capoeira*) stands with a history of use in slash-and-burn agriculture.

Figure 3 – Relationship between aboveground biomass (Mg ha^{-1}) and the age of abandonment of nine secondary-vegetation stands with a history of use in slash-and-burn agriculture. The model that best fits the relationship is: $\ln(\text{biomass}) = 2.051 + 1.042 \times \ln(\text{age})$; $r^2 = 0.959$.

Figure 4 – Relationship between aboveground biomass (Mg ha^{-1}) and an index related to land-use history (age of abandonment/time of use) in 15 secondary-vegetation (*capoeira*) stands in abandoned pasture.

Figure 5 – Relationship between aboveground biomass (Mg ha^{-1}) and an index related to land-use history (age of abandonment/(time of use + number of burns) in 15 secondary-vegetation (*capoeira*) stands in abandoned pasture. The equation that best fits the relationship is: $\ln(\text{biomass}) = 0.8\ \text{TB} + 0.9 \times \ln(\text{age}/(\text{time of use} + \text{number of burns}))$; $r^2 = 0.975$.

Figure 6 - Mean percent error (absolute value) of the estimated total biomass (Mg ha^{-1}) from the eight models described in Table 3 (as compared to the biomass measured this study through direct destructive methodology in 24 secondary-vegetation (*capoeira*) stands 1 to 15 years of age). Solid circles (●) indicate multispecific allometric models to estimate the biomass of trees derived from regressions with DBH and/or height as independent variables and whose sum was extrapolated to Mg ha^{-1}; Open circles (○) indicate models with regressions for predicting biomass (Mg ha^{-1}) with land-use history as an independent variable; bars represent the standard errors; the independent variables used by each author are shown in parentheses; details are given in Table 3.

Table 1. Monospecific allometric models with their statistical tests to estimate aboveground biomass (AGB in kg) of individuals of 13 species of secondary vegetation, with the independent variables diameter at breast height (dbh in cm) and height ht in m). The average error of estimate (absolute values) is for the percentage difference between the observed biomass per plant and that estimated by the model.

Species	Std (a)	dbh range	Regression equation	n	r^2	ME (b)	Significance (c)		SE (d)
Aegiphila integrifolia	In	1-16 cm	ln(AGB) = -2.180 + 2.582 × ln(ht × dbh)	11	0.925	28.9%	**α**	P < 0.0001	0.100
							β	P < 0.0001	0.24
Bellucia dichotomae & B. glossulariodes together	In	1-23 cm	ln(AGB) = -1.577 + 2.184 × ln(dbh)	35	0.942	27.8%	α	P < 0.0001	0.150
							β	P < 0.0001	0.095
Bellucia dichotoma	In	1-9	ln(AGB) = -3.092 + 1.543 × ln(dbh × ht)	21	0.905	35.9%	α	P < 0.0001	0.291
							β	P < 0.0001	0.115
	In	1-23 cm	ln(AGB) = -1.538 + 2.185 × ln(dbh)	30	0.938	26.9%	α	P < 0.0001	0.168
							β	P < 0.0001	0.106
Bellucia glossulariodes	In	1-15 cm	ln(AGB) = -1.641 + 2.169 × ln(dbh)	11	0.968	24.0%	α	P = 0.001	0.224
							β	P < 0.0001	0.159
Cecropia ulei	In	1-7 cm	ln(AGB) = -4.173 + 1.477 × ln(dbh)	138	0.944	20.2%	α	P < 0.0001	0.057
							β	P < 0.0001	0.031
	In and Out	1-7 cm	ln(AGB) = -4.163 + 1.489 × ln(dbh)	182	0.890	24.4%	α	P < 0.0001	0.069
							β	P < 0.0001	0.039
Couratari sp.	In	1-4 cm	ln(AGB) = -1.362 + 1.916 × ln(dbh)	11	0.868	23.4%	α	P < 0.0001	0.187
							β	P < 0.0001	0.236
Goupia glabra	In	1-6 cm	ln(AGB) = -1.523 + 1.926 × ln(dbh)	42	0.877	19.4%	α	P < 0.0001	0.092
							β	P < 0.0001	0.133
Lacistema grandifolium	In and Out	1-3 cm	AGB = -0.890 + 0.946 × dbh	12	0.743	33.9	α	P = 0,086	0.309
							β	P < 0.0001	0.176
Laetia procera	In	1-8 cm	ln(AGB) = -1.619 + 2.055 × ln(dbh)	21	0.962	21.1 %	α	P < 0.0001	0.133
							β	P < 0.0001	0.094
	In	1-8 cm	ln(AGB) = -2.765 + 1.263 × ln(dbh × ht)	21	0.961	19.7%	α	P < 0.0001	0.183
							β	P < 0.0001	0.981
	In	1-15 cm	ln(AGB) = -1.749 + 2.192 × ln(dbh)	50	0.982	12.7%	α	P < 0.0001	0.082
							β	P < 0.0001	0.991
Solanum rugosum	In	1-3 cm	ln(AGB) = -2.489 + 2.166 × ln(dbh)	23	0.861	34%	α	P < 0.0001	0.177

							β	P < 0.0001	0.270
Solanum rugosum	In and Out	1-3 cm	ln(AGB) = -2.224 + 1.908 × ln(dbh)	46	0.660	38.6%	α	P < 0.0001	0.127
							β	P < 0.0001	0.213
Trema micrantha	In	1-6 cm	ln(AGB) = -2.358 + 2.354 × ln(dbh)	33	0.962	13.8%	α	P < 0.0001	0.071
							β	P < 0.0001	0.084
Vismia cayennensis	In	1-9	ln(AGB) = -2.219 + 2.526 × ln(dbh)	32	0.972	16.1%	α	P < 0.0001	0.108
							β	P < 0.0001	0.078
	In	1-22 cm	ln(AGB) = -2.124 +2.431 × ln(dbh)	49	0.987	17.5%	α	P < 0.0001	0.075
							β	P < 0.0001	0.040
	In and Out	1-9	ln(AGB) = -2.062 + 2.412 × ln(dbh)	40	0.959	19.2%	α	P < 0.0001	0.7105
							β	P < 0.0001	0.081
Vismia guianensis	within standard	1- 5 cm	ln(AGB) = -1.6485 + 2.080 × ln(dbh)	150	0.908	21.7%	α	P < 0.0001	0.051
							β	P < 0.0001	0.7054
	within standard	5-15 cm	ln(AGB) = -2.029 + 2.327 × ln(dbh)	43	0.974	7.4%	α	P < 0.0001	0.127
							β	P < 0.0001	0.059
	within standard	1-15 cm	ln(AGB) = -1.706 + 2.160 × ln(dbh)	193	0.960	18.8%	α	P < 0.0001	0.036
							β	P < 0.0001	0.028
Vismia japurensis	within standard	1-5 cm	ln(AGB) = -1.689 + 2.239 × ln(dbh)	21	0.954	19.0%	α	P < 0.0001	0.113
							β	P < 0.0001	0.113
	Within and outside of standard	1-14 cm	ln(AGB) = -1.641 + 2.126 × ln(dbh)	81	0.986	19.4%	α	P < 0.0001	0.052
							β	P < 0.0001	0.029

(a) Std. (Architectural and health standard): In = within standard; Out = outside of standard.
(b) ME = Mean error of the estimate.
(c) Significance = Significance level of t for the coefficient.
(d) SE = Standard error.

Table 2. Multispecific regression models to estimate aboveground biomass (AGB in kg) of secondary vegetation individuals for a set of bushy species (excluding manioc), for a set of tree species (excluding the genus *Cecropia*, palms, vines, bamboo and wild bananas) and dead individuals that remain standing. The models were developed from biomass data measured with direct destructive methods in 24 secondary-vegetation plots between 1 and 15 years of age and with a use history of pasture and agriculture. The mean error of the estimate (absolute values) refers to the percentage difference between observed biomass per plant and that estimated by the model.

Species group	**Std. (a)**	**dbh range**	**Regression equation**	**n**	**r^2**	**ME (b)**	**Significance (c)**		**SE (d)**
Trees (excepting *Cecropia*)	In and Out	1-23 cm	ln (AGB) = -1.878 + 2.2154 × ln(dbh)	1370	0.943	25.4%	α	P < 0.0001	0.013
							β	P < 0.0001	0.086
	In	1-23 cm	ln (AGB) = -1.869 + 2.231 × ln(dbh)	1128	0.963	20.3%	α	P < 0.0001	0.086
							β	P < 0.0001	0.013
Bushes	In and Out	1-4 cm	AGB = -0.253 + 0.3611 × dbh	74	0.703	40.3%	A	P < 0.0001	0.048
							β	P < 0.0001	0.009
Standing dead plants		1-5 cm	ln (AGB) = -2.172 + 1.803 × ln(dbh)	40	0.623	33.1%	α	P < 0.0001	0.185
							β	P < 0.0001	0.227

(a) Std. (Architectural and health standard): In = within standard; Out = outside of standard
(b) ME = Mean error of the estimate.
(c) Significance = Significance level of t for the coefficient.
(d) SE = Standard error.

Fig 1

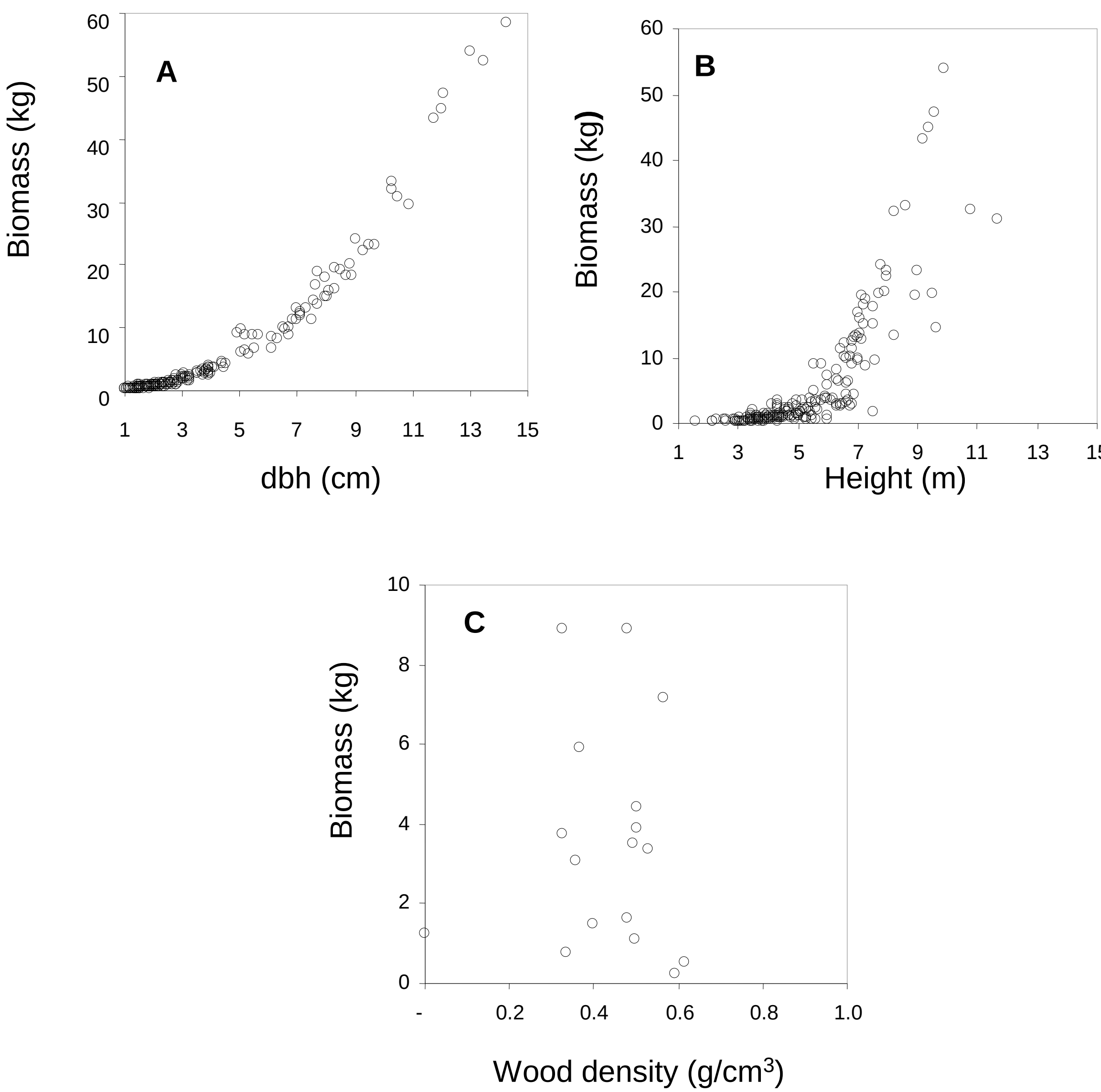
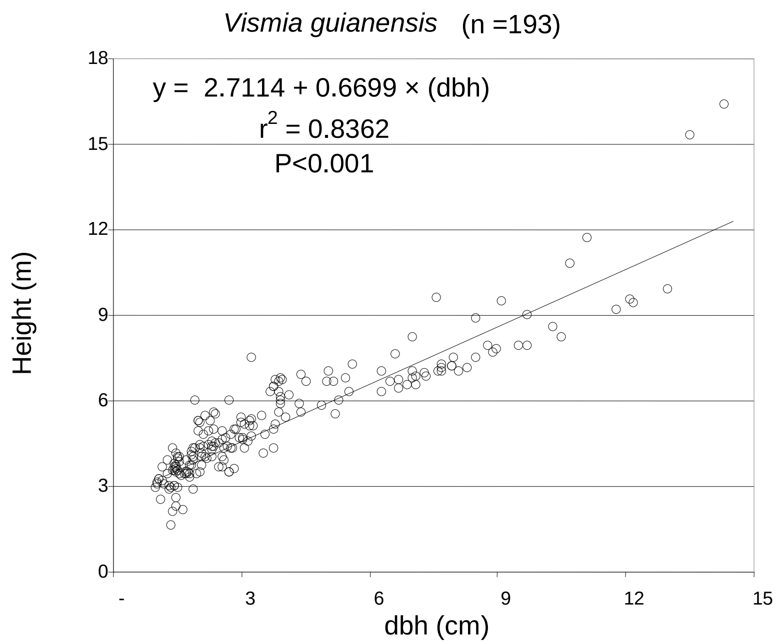

A
Biomass (kg)
dbh (cm)
B
Biomass (kg)
Height (m)
C
Biomass (kg)
Wood density (g/cm³)

Fig 2



Vismia guianensis (n =193)
y = 2.7114 + 0.6699 × (dbh)
r2 = 0.8362
P<0.001
18
15
12
9
6
3
0
-
3
6
9
12
15
Height (m)
dbh (cm)