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Carbon accumulation in the biomass and soil of different aged secondary forests in the humid tropics of Costa Rica

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ABSTRACT

Efforts are needed in order to increase confidence for carbon accounts in the land use sector, especially in tropical forest ecosystems that often need to turn to default values given the lack of precise and reliable site specific data to quantify their carbon sequestration and storage capacity. The aim of this study was then to estimate biomass and carbon accumulation in young secondary forests, from 4 and up to 20 years of age, as well as its distribution among the different pools (tree including roots, herbaceous understory, dead wood, litter and soil), in humid tropical forests of Costa Rica. Carbon fraction for the different pools and tree components (stem, branches, leaves and roots) was estimated and varies between 37.3% (±3.3) and 50.3% (±2.9). Average carbon content in the soil was 4.1% (±2.1). Average forest plant biomass was 82.2 (±47.9) Mg ha^{-1} and the mean annual increment for carbon in the biomass was 4.2 Mg ha^{-1} yr^{-1}. Approximately 65.2% of total biomass was found in the aboveground tree components, while 14.2% was found in structural roots and the rest in the herbaceous vegetation and necromass. Carbon in the soil increased by 1.1 Mg ha^{-1} yr^{-1}. Total stored carbon in the forest was 180.4 Mg ha^{-1} at the age of 20 years. In these forests, most of the carbon (51–83%) was stored in the soil. Models selected to estimate biomass and carbon in trees as predicted by basal area had R^2 adjustments above 95%. Results from this study were then compared with those obtained for a variety of secondary and primary forests in different Latin-American tropical ecosystems and in tree plantations in the same study area.

1. Introduction

Growing forests and tree plantations and their soils are major sinks of atmospheric carbon (FAO, 2006; IPCC, 2007; Saugier and Pontailler, 2006; Schimel et al., 2001), and thus the influence of forests in the global carbon cycle is now widely recognized (Basu, 2009; Bonan, 2008; González et al., 2008). Forest vegetation captures atmospheric CO_2 through photosynthesis and stores it mainly in hard biomass (wood) with a slow turnover rate of 14–19 years for native forests in Chile (Gayoso and Guerra, 2005), around 50–100 years in the Amazon (Vieira et al., 2005) and an average of 50 years according to Reeburgh (1997). This rate has been estimated for one to two decades for secondary forests in Puerto Rico when considering litter (Ostertag et al., 2008). Atmospheric carbon incorporation rates into the biomass or soil tend to decrease with forest age, being it higher at young or intermediate ages (Gayoso and Guerra, 2005; Ostertag et al., 2008; Saynes et al., 2005). Forests also mobilize atmospheric carbon through plant respiration and organic material decomposition, although these losses are usually less than the gains. An exception is old growth forests or forests suffering from acute degradation, where losses can exceed gains (CATIE, 2002). Forests, in addition, may transfer organic material towards the water table or groundwater or other aquatic ecosystems (FAO, 2002; Percy et al., 2003).

The world's forest cover is now around 4 billion ha (0.59 ha per capita) (FAO, 2009). Secondary forests (those regenerating largely through natural processes after significant human and/or natural disturbance of the original forest vegetation; Chokkalingam and de Jong, 2001) represent 35% of the tropical forests (Emrich et al., 2000), approximately 850 million hectares (FAO, 2006), but accounts on land area under this type of forest cover are hard to assess. For example, in Costa Rica, the area of secondary forests under different succession stages is uncertain and several estimates have been provided during the last years. Joyce (2006) provided an estimate of 793,811 ha in 2004, according to MINAE-SINAC (2007) there are 586,967 ha and in the most recent study, up to 900,000 ha were found (Costa Rica, 2010). In any case, it is likely that this ecosystem is increasing its cover promoted by the instability of prices from agricultural products and the migration of

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inhabitants from rural areas to more urban areas (Aide and Grau, 2004; Grau and Aide, 2008; Rey Benayas, 2005).

Adding to this uncertainty, when accounting for the carbon absorption and storage capacity of forest ecosystems, many authors agree on the weaknesses from current estimates (Chave et al., 2004; Sarmiento et al., 2005). Given the lack of site specific data, these estimates have to be performed using generic values on the amounts of biomass, carbon in the biomass or generic allometric equations to determine biomass and carbon for a given forest ecosystem. This procedure will hardly reflect in these accounts the interactions between environmental and anthropogenic factors that cause variations in the carbon concentrations within the biomass (with global variations ranging from 1 to 35 t CO_2 ha^{-1} yr^{-1}; IPCC, 2007) (Sarmiento et al., 2005; Keith et al., 2009) and a range of estimated emissions from the land-use change as wide as 0.5–2.7 GtC for the 1990s (Ravindranath and Ostwald, 2007).

In the Latin American context, the majority of studies document growth in biomass and carbon storage in primary forests, mainly in the woody material (Acosta et al., 2002; Schlegel et al., 2001; Segura et al., 2000). Studies on secondary forests are scarcer (Feldpausch et al., 2007; Fonseca et al., 2008; Herrera et al., 2001) and even more, the quantification of total plant biomass and carbon, including roots, has not been a common practice, and is even rarer for secondary forests.

Under this context, we conducted a research in the Costa Rican Caribbean region, with the aim of estimating the amount of biomass and carbon accumulated and stored in young secondary forests, as well as its distribution among the different pools (tree, herbaceous vegetation, necromass, and soil). Since precise estimations of all biomass and carbon pools are expensive and time consuming, we developed models to estimate biomass and carbon stored by area unit, so simple field measurements allow for these estimations at these ecosystems in the future. In addition, the carbon fraction in the biomass was determined for the different components of the biomass.

2. Materials and methods

2.1. Study area

This research was developed in the Costa Rican Caribbean region, which corresponds to a very humid tropical forest life zone, according to Holdridge's Life Zone classification system Holdridge (1967). The altitude ranges between 50 and 350 m asl. Predominating climate is humid to very humid, hot to very hot, with or without a dry season of <25 intermittent days with water deficit per year (Herrera, 1985; Mena, 2007). The mean annual precipitation varies between 3420 and 6840 mm and mean annual temperature between 25 and 27 °C. Forests are found on soils that are Ultisols and Inceptisols, with <35% base saturation, these are deep, well drained, red or yellow in color and with relatively low fertility. Both of these soil types are located on land with slopes that range between 2% and 15% (ITCR, 2004).

2.2. Establishment of sampling plots

Seven sites were selected within the study area with secondary forests that range between 4 and 20 years of age. Selection criteria was based on access to the forests (landowners willingness to support research), landowners knowledge of the forest age and an appropriate distribution and representativeness of ages. These forests were therefore found in private lands which were mostly abandoned pasture lands and for which age was determined based on the landowner's knowledge of land abandonment. In each site, two to six 500 m^2 rectangular sampling plots were established to estimate forest biomass. The number of plots at each site depended on the variation of the secondary forest regeneration age (at least one plot per identified age) and the heterogeneity of the secondary forest (i.e., if one coetaneous secondary forest showed a heterogeneous vegetation structure, this was measured through the establishment of two or more plots). A total of 38 plots were established, out of which 10 plots were re-measured 2 years after the first measurement in order to complete an appropriate age distribution for a total of 48 plots sampled. Some forests with similar ages were grouped to simplify analysis. These correspond to ages 4.5 and 6.5 (Table 2), which compile data averaged for ages 4–5 and 6–7 accordingly.

Each 500 m^2 plots included four 1 m^2 and one 25 m^2 subplots to sample particular biomass compartments (see below). In addition, 11 plots that represented a baseline from which secondary succession started were also sampled. These sites were within the farms, adjacent to secondary forests sampled and where the current land use is still pasture land. Baseline vegetation consisted mostly of grasses from the Poaceae family.

2.3. Biomass estimation

2.3.1. Aboveground tree biomass

Aboveground tree biomass is usually determined through the selection of a single tree based on the dbh. MacDicken (1997) recommends the selection of a tree with mean basal area, Schlegel et al. (2001) recommends the random selection of one tree per diametric class of the most abundant species in each class. For this study, the selection of trees to be harvested was based on the Importance Value Index (IVI), the IVI being the sum of abundance, frequency and dominance or basal area expressed in relative values (Krebs, 1985). In each plot, every individual was classified into 5 cm interval diametric classes, and the species with the highest Importance Values Index (IVI) were determined for each class. In each sampling plot, all woody plants with a diameter at breast height (dbh) $\geqslant$2.5 cm were measured. These accounted for a total of 6984 individuals, which were identified to the species (66.6%), genera (30.3%) and family level (0.38%) or remained unknown (2.7%). In each plot, every individual was classified into 5 cm interval diametric classes, and selected a mean tree for each class as a sample. A total number of 193 trees corresponding to 35 different species whose diameter varied between 2.8 and 28.2 cm were sampled. The biomass was determined through field measurements for weight for each tree component (leaves, branches and stem).

2.3.2. Belowground tree biomass

Belowground tree biomass in this study mainly refers to the structural or "anchor" roots and all of the fine roots attached to the main root after harvesting. Roots with a diameter > 5 mm (according to the classification proposed by Sierra et al. (2001)) were estimated through the excavation and extraction of the root system for the average selected trees. Excavation and extraction was carried out with a retro-excavator or trencher, agricultural tractor and/or manually with a chain hoist. These roots were then washed in the field and weighed once they were air dry for 1–2 h.

2.3.3. Biomass in herbaceous vegetation, small woody material and seedlings

Grasses, lianas, ferns, shrubs and some tree seedlings with a dbh <2.5 cm, were measured in 1 × 1 m subplots located in every corner of the main 500 m^2 plot. In each 1 m^2 subplot all plant material was harvested to ground level, all four subplots were grouped into one sample and weighed in the field.

Table 1
Carbon fraction (%) in the biomass and soil carbon content (%) in different compartments of young secondary forests in the humid tropics of Costa Rica.

Statistics	Stem	Branches	Leaves	Roots	Herbaceous vegetation	Large necromass	Fine necromass	Soil
X	47.9	47.3	37.3	47.5	43.5	50.3	41.1	4.1
SD	3.9	3.3	3.3	4.4	1.9	2.9	2.4	2.1
n	193	191	193	193	58	48	48	59

X = average, SD = standard deviation, *n* = number of samples.

Table 2
Accumulated biomass and carbon (numbers in bold correspond to carbon) in secondary forests and their distribution in the different biomass compartments and soil. All expressed in Mg ha^{-1} ± standard deviation.

Age	Number of sampling plots	*G* (m^2/ha)	Total biomass	Tree biomass	Fine necromass	Herbaceous vegetation	Large necromass	C soil	MAI soil
0	11		2.5 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	2.53 ± 0.3	0.0 ± 0.0		
			1.15 ± 0.1	**0.0 ± 0.0**	**0.0 ± 0.0**	**1.15±0.1**	**0.0 ± 0.0**	**99.1 ± 38.5**	
4.5	6	8.6 ± 5.3	44.9 ± 38.1	37.3 ± 36.6	3.6 ± 2.0	2.2 ± 1.4	1.9 ± 1.8		
			17.1 ± 12.0	**13.2 ± 11.2**	**1.9 ± 0.8**	**1.1 ± 0.4**	**0.9 ± 5.1**	**95.1 ± 12.5**	**1.6 ± 0.7**
6.5	12	9.8 ± 5.0	40.5 ± 16.7	32.8 ± 16.9	2.1 ± 1.5	2.8 ± 2.6	2.9 ± 4.5		
			19.4 ± 8.0	**15.7 ± 7.8**	**0.8 ± 0.6**	**1.2 ± 1.1**	**1.7 ± 2.2**	**96.0 ± 21.6**	**0.6 ± 0.5**
8	4	15.1 ± 8.1	86.9 ± 36.3	79.1 ± 39.4	4.1 ± 0.6	1.9 ± 2.9	1.9 ± 1.4		
			36.4 ± 16.5	**33.0 ± 17.7**	**1.7 ± 0.2**	**0.8 ± 1.2**	**1.0 ± 0.8**	**90.1 ± 11.1**	**0**
10	5	21.4 ± 8.5	174.5 ± 16.4	127.5 ± 47.7	6.7 ± 3.0	1.2 ± 0.8	39.0 ± 45.6		
			87.1	**65.4 ± 26.6**	**3.0 ± 1.5**	**0.5 ± 0.3**	**18.2 ± 20.4**	**90.4 ± 11.2**	**0**
12	15	18.7 ± 4.8	104.0 ± 37.0	88.2 ± 37.3	6.3 ± 3.6	1.4 ± 0.9	8.1 ± 14.3		
			49.2 ± 17.1	**41.9 ± 17.2**	**2.6 ± 1.4**	**0.6 ± 0.4**	**4.0 ± 7.2**	**114.8 ± 31.9**	**2.3 ± 2.1**
18	4	16.9 ± 3.9	67.2 ± 7.3	52.9 ± 2.6	5.9 ± 2.2	2.0 ± 0.7	6.4 ± 8.3		
			31.7 ± 4.9	**24.9 ± 1.6**	**2.5 ± 1.2**	**0.8 ± 0.3**	**3.5 ± 4.6**	**115.1 ± 32.1**	**1.4 ± 1.7**
20	3	18.4 ± 1.3	102.3 ± 19.3	92.8 ± 20.8	3.4 ± 1.4	1.3 ± 0.9	4.8 ± 7.4		
			47.3 ± 7.4	**42.9 ± 6.0**	**1.4 ± 0.6**	**0.6 ± 0.4**	**2.4 ± 3.7**	**133.1 ± 28.5**	**1.7 ± 1.4**

2.3.4. Necromass

Necromass or dead woody material found at ground level was divided into fine necromass (litter and woody material <2 cm in diameter) and large necromass (dead woody material $\geqslant$2 cm in diameter). Fine necromass was estimated at four 0.5 $\times$ 0.5 m subplots that were randomly distributed throughout the 500 m^2 plot; these four samples were grouped into one sample for analysis. Large necromass was estimated at one 5 $\times$ 5 m subplot that was randomly placed within the 500 m^2 plot. The collected material was weighed in the field.

2.4. Soil organic carbon and carbon fraction in the biomass

The total amount of carbon stored in the soil was quantified based on the soil's carbon content, bulk density and sampling depth. A total of four 30-cm depth soil samples were randomly selected within each main plot, extracted and mixed together in order to obtain a sample of approximately 1 kg. Bulk density was determined through the cylinder method (MacDicken, 1997), collecting one cylinder per plot.

2.5. Carbon fraction analysis in plant material and soil

For every sample weighed in the field, an approximately 1 kg sub-sample was collected and taken to the laboratory in order to determine the carbon fraction. Each sub-sample of the different components of the biomass was taken to the lab and dried in an oven at 60 °C for 72 h to estimate its dry matter content (DMC). Soil samples were dried at 55 °C for 3 days and subsequently ground and run through a 240-μm sieve. Carbon content in the plant biomass and soil was determined following the methods by Pregl and Dumas (Bremner and Mulvaney, 1982) in an auto-analyzer (Perkin-Elmer series II, CHN/S 2400, Norway Co.).

2.6. Increases in the carbon content in plant biomass and soils

The Mean Annual Increment (MAI) was calculated for the biomass and for the carbon in the biomass and soil as MAI = B or C/*t*, where B is biomass, C is carbon, both expressed in Mg ha^{-1}, and *t* is the number of years (Prodan et al., 1997). Although the procedure to determine MAI for soil is essentially the same, for this pool, the amount of carbon at the baseline scenario should be subtracted from the total carbon at each year and then divided by the number of years. For this same reason and considering that results from different sites are averaged into one single value, soil MAI values resulting negative due to a baseline average higher than the average for carbon content, were expressed as zero.

2.7. Models to estimate biomass and carbon

Models were adjusted using the method of ordinary least squares (Fonseca et al., 2009). Approximately 25 models were tested for total tree biomass (Mg ha^{-1}), total forest biomass (Mg ha^{-1}) and total carbon in the biomass (Mg ha^{-1}). The methodology presented by Salas (2002) and Segura and Andrade (2008) was followed in order to determine the best fit equation. The selected models with logarithmic transformations were later corrected using a correction factor (CF) as explained by Sprugel (1983). The suggested equation to estimate the correction factor is: CF = exp(SSE^2/2), where: SSE = estimated standard error by the regression.

2.8. Forest composition, stand structure and biomass accumulation

To evaluate the effects of stand composition over biomass and/or carbon accumulation, sampling units were grouped by age; 4–5, 6–7, 8, 10, 12, 18 and 20 years. The specie with the highest IVI per diametric class and the wood specific density for each of these species was determined (WSD in gr/cm^3) according to Chave et al. (2006). Wood specific density was classified as high (WSD ⩾ 0.48 gr/cm^3) and low when values were found below this value. For each sampling unit, a diametric distribution was created and the abundance (trees ha^{-1}) per diametric class was determined.

3. Results

3.1. Carbon fraction in the biomass and soil carbon content

The carbon fraction for the more lignified biomass components (stem, branches, roots and large necromass) in secondary succession of 4–20 years, varied between 47.3% (±3.3) and 50.3% (±2.9). The carbon fraction for leaves, herbaceous vegetation and fine necromass (litter) varied between 37.3% (±3.3) and 43.5% (±1.9). The average across biomass compartments was 46.8% ± 4.0. Soil had a carbon content of 4.1% (±1.9; Table 1).

3.2. Carbon accumulation in plant biomass

Total biomass increased with the age of the secondary succession and had a positive correlation (Fig. 1). The increase in biomass was fast during the first 10 years, when total biomass averaged 174.5 ± 16.4 Mg ha^{-1}. It then decreased with lower values found in secondary forests older than that age (Fig. 1; Table 2). The average total biomass for all different ages was 82.2 ± 47.9 Mg ha^{-1}. The mean annual increments for total biomass and carbon in the biomass were 8.9 and 5.3 Mg ha^{-1} yr^{-1}, respectively.

Most of the carbon in the forest plant biomass was stored in the trees, with an average of 80.1 ± 15.3% at all different ages, followed by necromass (15.8 ± 13.0%) and herbaceous vegetation (4.2 ± 5.5%) (Fig. 1; Table 2). There were no significant differences between the amounts of biomass and carbon in the biomass in compartments other than trees (Table 2). Within the tree compartments, carbon was highest in the stem (58.4 ± 11.8%), and lower in the branches (18.4 ± 7.3%), roots (17.9 ± 6.4%) and leaves (5.3 ± 1.7%; Table 3). The aboveground to belowground ratio was marginal and negatively correlated with forest age ($r = -0.27$, $P = 0.06$, $n = 48$).

3.3. Carbon accumulation in the soil

The amount of carbon in the soil was positively correlated with the age of the secondary forest, but this was a relatively weak relationship (Fig. 1). The increase of carbon in the soil was 1.09 Mg ha^{-1} yr^{-1}. At all ages, the amount of carbon accumulated in the soil was higher than the amount of carbon stored in total biomass (Fig. 1; Table 2).

At the forest level (biomass and soil), the carbon accumulated increased with forest age (Fig. 1; Table 2). In recently established forests, where the biomass mainly corresponded to herbaceous vegetation, 98.8% of the total carbon was stored in the soil. However, the relative amount of the total forest carbon in the soil decreased rapidly as the succession progressed on, and 73.77% of total carbon was stored in the soil in 20-year old forests (Fig. 1).

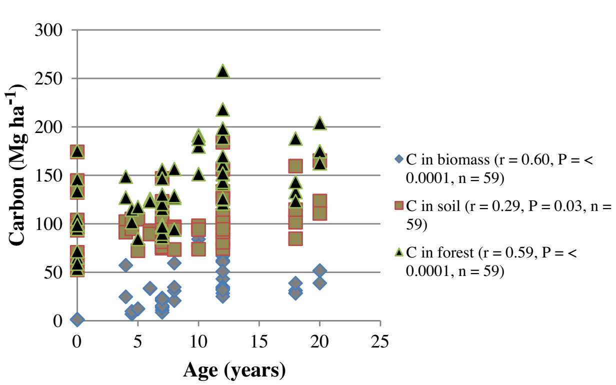

Fig. 1. Carbon accumulation in secondary forests of different ages and its distribution in the biomass and soil.

3.4. Biomass and carbon models

Three models were selected to estimate biomass and carbon in the biomass that were highly predictive (Table 4). These models had adjusted R^2 above 95% and the significance levels was $p < 0.01$; the models' standard errors were low and showed a normal distribution. The use of a correction factor (CF) increases the amount of estimated biomass and carbon by <5%. The models that used age and diameter at breast height as predictive variables of total biomass and carbon did not show a good model fit (results not shown).

3.5. Forest composition, stand structure and biomass accumulation

Sites with forest regeneration below 7 years had the highest amount of low WSD and an average tree biomass between 32.8 and 37.3 Mg ha^{-1} in spite of the high number of trees ha^{-1} (approximately 3400 trees ha^{-1}). In forests between 4 and 5 years, only 33% of species in all diametric classes showed high WSD. At 6–7 year old forests, this relationship increases throughout all diametric classes, with 63% of species classified as having a high WSD. The most common species found at this age were *Dipteryx panamensis*, *Colubrina spinosa*, *Croton smithianus*, and *Casearia arborea*. At 8 and 12 year old forests, species with high WSD such as *Pentaclethra macroloba*, *Miconia sp*. and *Casearia arborea* are above 65% of all species found within all diametric classes. These forests, too, show high tree densities (between 2638 and 4130 trees ha^{-1}; Table 5) and accumulate tree biomass in the order of 79.1 and 127.5 Mg ha^{-1} (Table 2). This same trend, high amount of species with high WSD can be observed at 18 year old forests (66.7% of all species found within all diametric classes) but not so at 20 years, were species with high WSD decrease to 58.3%. However, in both age classes (18 and 20) there was a decrease in the number of trees ha^{-1} (1755 and 1687 trees ha^{-1}, respectively; Table 5) and in the amount of tree biomass found (52.9 and 92.8 Mg ha^{-1}, respectively; Table 2).

4. Discussion

4.1. Carbon content in the biomass of secondary forests

In this study we estimated the amount of accumulated carbon in the biomass for the different components of young secondary forests of the Costa Rica Caribbean Region. Few previous studies have estimated the precise values of the amount of carbon found in the biomass of secondary forest species, and thus to transform the amount of dry biomass into carbon a 0.5 conversion factor (Hoen and Solberg, 1994; Husch, 2001; Sarmiento et al., 2005) is generally used. For the studied forests, the lowest carbon fractions of plant biomass corresponded to those components with less lignin, such as fine necromass, leaves and herbaceous vegetation, while large necromass, stem, roots and branches had higher carbon concentrations (Gayoso and Guerra, 2005; Gifford, 2000). Other studies have not found differences in the carbon content of the different tree components (Segura et al., 2000). Furthermore, higher carbon concentrations in components such as leaves have been reported (Gifford, 2000). The results obtained in this study are found within the limits reported for forest plantations in the same region (Cubero and Rojas, 1999; Fonseca et al., 2009).

Table 3
Biomass and carbon in the different components of total biomass, trees, and ecosystem.

Statistics	Total biomass (Mg ha^{-1})	Necromass (%)	Herbaceous vegetation (%)	Litter (%)	Tree biomass (%)			
					Leaves	Branches	Stem	Roots
Total biomass components								
n	48	48	48	48	48	48	48	48
X	81.98	8.97	4.51	7.10	4.77	14.35	46.13	14.17
SD	47.90	12.59	5.98	5.94	2.10	6.89	11.97	5.48
Carbon in tree biomass (%)								
n					48	48	48	48
X					5.32	18.37	58.38	17.93
SD					1.68	7.32	11.76	6.35
Carbon in the ecosystem								
	Ecosystem (Mg ha^{-1})				Tree biomass (%)		Soil carbon (%)	
n	48	48	48	48	48		48	
X	143.16	2.87	0.68	1.35	20.82		74.29	
SD	36.94	5.33	0.67	0.83	10.48		11.98	

X = average, SD = standard deviation, n = number of samples.

Table 4
Models selected for the estimation of biomass and carbon accumulated in secondary forests.

Model	R^2 aj (%)	SEE	N	CF
Bt = exp(1.06839 + 0.80802 × $\sqrt{G}$	95.7	0.310	48	1.05
CBa = exp(0.15004 + 0.800996 × $\sqrt{G}$	97.8	0.216	48	1.02
CBt = exp(0.272739 + 0.816253 × $\sqrt{G}$	96.0	0.299	48	1.05

Bt = total biomass (Mg ha^{-1}), CBa = carbon in the tree biomass (Mg ha^{-1}), CBt = carbon in the total biomass (Mg ha^{-1}), G = basal area m^{2}ha^{-1}, R^2 aj = adjusted coefficient of determination; exp (natural log base = 2.718271), n = sample size, SEE = model's standard error, CF = correction factor.

4.2. Carbon accumulation in secondary forests

The maximum biomass accumulation in this study and the mean annual increment (174.5 Mg ha^{-1} and 8.9 Mg ha^{-1} yr^{-1}, respectively) are found within the range reported for secondary tropical forests by other studies (Chacón et al., 2007; Marín et al., 2007; Yan et al., 2007). The average MAI for biomass, excluding roots, from all these studies was 7.83 Mg ha^{-1} yr^{-1}.

We found that the amount of carbon stored in the soil represented 74.3% of the total carbon in the forest, 51.5% higher than the biomass. Other studies in tropical areas have found that the amount of soil carbon was between 50% and 75% of the total forest carbon (Fonseca et al., 2008; Jandl, 2006; Lagos and Vanegas, 2003).

The average increase and the percentage of organic carbon in the soil reported by other studies, for primary and secondary tropical forests, are 0.5–2.0 Mg C ha^{-1} yr^{-1} and 3.34%, respectively (Feldpausch et al., 2007; Fonseca et al., 2008; Liu et al., 2006), are similar to the values of 1.09 Mg ha^{-1} yr^{-1} and 4.2% found in this study. In spite of the contribution that soil plays in the ecosystem's total carbon, approximately 75% of the references cited by this study did not evaluate this carbon pool, due to its difficulty and high costs (Brown et al., 1989; de Jong et al., 2000; MacDicken, 1997).

There is some controversy with regards to the role of land use change and the accumulation of carbon in the soil, where previous land use is said to be a determining factor in either soil carbon accumulation or loss (Post and Kwon, 2000; Guo and Gifford, 2002; IPCC, 2007). Considering that pasture lands contain a higher amount of fine roots that incorporate more carbon to the soil due to a fast decomposition rate as opposed to a more lignified radical system from trees, Guo and Gifford (2002) have reported for carbon loss from this pool when changing from pastures to secondary forests. Other studies have found an increase in carbon and thus recognize that soil carbon tends to increase as the succession moves forward due to the contribution of organic matter from roots and decomposing detritus (Hughes et al., 1999; Powers and Veldkamp, 2005; Schedlbauer and Kavanagh, 2008; Sierra et al., 2001; Veldkamp et al., 2003). Still, other studies have failed to find differences among different age groups (Gamboa et al., 2008; Ostertag et al., 2008; Tschakert et al., 2007).

Accordingly, we did find a positive but low correlation between the amount of soil carbon and the age of the forest, in contrast with the high correlation found between biomass and forest age (Fig. 1). The low correlation between soil carbon and forest age can be attributed partly to the slow incorporation of carbon into the soil (Gamboa et al., 2008; McGrath et al., 2001; Robert, 2002; Saynes et al., 2005; Singh et al., 2007; Turner et al., 2005) together with the young age of the studied forests. However, as reported by other authors, previous land use, the number of years under the previous land use, the stage of the succession, distance from seed sources and intervention or management, among others (Hughes et al., 1999; Mesquita, 2000) may all be factors, that individually or in a combination, determine the amount of carbon found at the soil. In this particular case, given that these secondary forests have grown in degraded, over pastured and more compacted lands, we believe that asides from the reasons reported by other studies, there might also be an effect by differences on bulk density from these soils and those found under secondary forests. However, this assumption still needs to be proven.

4.3. Comparison with tree plantations

Fonseca et al. (in press) determined the carbon accumulated in the biomass and soil of managed forest plantations of comparable ages (from 0 to 16 years of age), found within the same region and therefore under similar conditions. Furthermore, these also followed the same land use pattern, changing from pasture lands to forest lands. MAI values for these ecosystems were of 7.1 MgC ha^{-1} yr^{-1} in the biomass of *Vochysia guatemalensis* and 5.3 MgC ha^{-1} yr^{-1} in *Hieronyma alchorneoides* plantations. For these same plantations, increases from carbon in the soil were 1.7 and 1.3 Mg ha^{-1} yr^{-1}, respectively. These results show how forest plantations (without taking into account biomass from thinnings and in spite of these being 4 years younger) have almost twice the ability to store carbon in the biomass when compared to secondary forests under similar conditions and an approximately 20% more with regards to soil carbon. At an ecosystem level, MAI for total carbon in forest plantations was of 8.7 and 6.5 MgC ha^{-1} yr^{-1}, higher than the 5.3 MgC ha^{-1} yr^{-1} found in

Table 5
Species with the highest IVI per diametric class, average number of trees ha^{-1} by age class, wood specific density (WSD = gr/cm^3, a WSD $\geqslant$ 0.48 gr/cm^3 is considered high and are shown in parenthesis and bold letters).

Plot	Age (years)	Diametric class (cm)/species[a] −5	5–9.99	10–14.99	15–19.99	+20	Trees ha^{-1}	No.	Species	WSD
1–6	4–5	(**4–4–27**) 5–25–25	**(27)** 16–32–33–25–25	(**14**) 20–32–37–33	16–16	(**4–4**)	3427	1	*Anaxagorea grassipetala*	0.48
								2	*Anthodiscus chocoensis*	0.7
								3	*Bactris sp.*	–
								4	*Casearia arborea*	0.57
7–18	6–7	(**21–21–22–27–27–27–27–27–27–27**) 25–25	(**21–27–27–27–27–7**) 20–25–25–25–6–28	(**11–14–14–15–7–34–7**) 20–30–28–6–28	(**11**) 16–5–26		3460	5	*Cecropia insignis*	0.31
								6	*Cecropia obtusifolia*	0.31
								7	*Colubrina spinosa*	0.49
								8	*Cordia alliodora*	0.53
								9	*Croton draco*	0.48
								10	*Croton schiedeanus*	0.48
								11	*Croton smithianus*	0.48
19–22	8	(**24–7**) 25–25	(**4**–**24**–**7**) 24	(**24–24–24**)17	**(24–24–24–19)**	**(19)**	2555	12	*Cupania sp.*	0.64
								13	*Dendropanax arboreus*	0.42
23–27	10	**(7–4–18–24–21)**	**(7–18–24–18)** 31	**(11–11)** 13–31–20	**(7–18–11–11)** 31		4130	14	*Dipteryx panamensis*	0.85
								15	*Gliricidia sepium*	0.58
								16	*Goethalsia meiantha*	0.35
28–42	12	**(24–4–24–24–21–4–21–3–21–21–4–4–21–4)** 25	**(24–24–24–24–24–24–9–21–21–21–4–4–24)** 16–31	**24–24–24–24–24–24–21–21–4–4–24)** 5–20–31	**(24–35–24–24–24–9–1–3–4–11–11–11)**–6–36–31	**(24–4–24)** 36	2368	17	*Hampea appendiculata*	0.25
								18	*Hirtella sp.*	0.8
								19	*Inga sp*	0.49
								20	*Jacaranda copia*	0.35
								21	*Miconia sp.*	0.63
								22	*Palicurea guianensis*	0.54
								23	*Parmentiera cereifera*	–
								24	*Pentaclethra macroloba*	0.61
43–46	18	**(29–4)** 25–17	**(8–10–11)** 17	**(8–12–11)** 17	**(19–24)** 17–17	**(2–19)**	1755	25	*Piper adecuali*	0.3
								26	*Pourouma minor*	0.44
								27	*Psychotria sp.*	0.56
47–49	20	**(4–21)** 25	**(4–8)** 23	**(11–8)** 17	**(11)** 17	17	1687	28	*Rollinia sp.*	0.36
								29	*Rondelethia aspera*	0.5
								30	*Sapium glandulosum*	0.44
								31	*Saurauria sp.*	0.44
								32	*Turpinia occidentalis*	0.34
								33	*Vernonia patens*	–
								34	*Virola sp.*	0.5
								35	*Vismia ferruginea*	0.49
								36	*Vochysia ferruginea*	0.4
								37	*Vochysia guatemalensis*	0.35

[a] Numbers stand for species according to the list at the right.

secondary forests from this study. This can be partly explained by the effect of silvicutural activities aimed at increasing the amount and quality of forest productivity (Daniel et al., 1982; Kerr and Morgan, 2006; Wadsworth, 2000), therefore increasing carbon accumulation and organic material incorporated to the soils.

4.4. Models to estimate biomass and carbon

In the tropics, models to estimate biomass and carbon tend to show good R^2 adjustments when relating the biomass to diameter, basal area and/or height of individual trees (Fonseca et al., 2009). Most previously published models have been used to estimate biomass and carbon per tree and/or tree component (Acosta et al., 2002; Brandeis et al., 2006; Gaillard et al., 2002; Litton and Kauffman, 2008; Lagos and Vanegas, 2003; Segura and Kanninen, 2005) but we have not found models to estimate biomass and carbon per area unit. Where in doing so, our results from the tested models show a good adjustment ($R^2_{aj} > 95\%$) equal to or above reported by other works, which we mainly attribute to our high number of samples distributed over a wide range of ages. In this work, the tested models using age as the predicting variable for biomass and carbon did not show good R^2 adjustments, a behavior that has been a common trend in other studies (Feldpausch et al., 2004). Overall, the good adjustment of the selected models to estimate biomass and carbon per hectare using simple field variables such as basal area represents an important advance towards the precise and reliable quantification of carbon accumulation in tropical secondary forests.

4.5. Forest composition, stand structure and biomass accumulation

Stand composition and structure of the studied forests can be related to the accumulated biomass and/or carbon. Fast growth species (pioneers) have low WSD (Chave et al., 2006) and therefore low amounts of biomass. At the same time, given that most tree components are less lignified, these show a lower carbon concentration (Fonseca et al., in press; Gayoso and Guerra, 2005; Gifford, 2000). However, and in accordance with current knowledge on succession dynamics, there is an accelerated increase in the biomass during the first succession stages which then decreases due to mortality of heliophilous or pioneer species and stabilizes when these forests reach intermediate or advanced stages (Emrich et al., 2000; Fonseca, 2006; Müller, 2002; Spittler, 2002) with a higher number of late heliophilous and sciophilous species.

In our study, MAI results for biomass support this knowledge with results that decrease with the age of the forest (i.e. 8.3, 7.4 and 4.6 at 4.5, 12 and 20 years, respectively) and with peaks at certain moments (e.g. age 10) due to site specific conditions. Differences in stand structure and composition might result from site specific conditions and explain these peaks. In terms of the differences in biomass accumulation that are attributable to forest composition, WSD could be the most significant. However, given that the selected species to quantify the biomass of forests above 8 years, all show similar WSD and that at least 58% of all species are considered as being high throughout all age and diametric classes, the effect of composition on biomass accumulation might not be that significant. From our results, it becomes evident that on this regard, the accelerated increases in the biomass in the age classes from 4 to 12 years and the decrease at 18–20, are in fact mostly determined by stand structure, were differences in the amount of trees ha^{-1} are markedly decreasing with age (Table 5).

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