

Carbon accumulation in aboveground and belowground biomass and soil of different age native forest plantations in the humid tropical lowlands of Costa Rica

William Fonseca · Federico E. Alice · José María Rey-Benayas

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Abstract Generic or default values to account for biomass and carbon accumulation in tropical forest ecosystems are generally recognized as a major source of errors, making site and species specific data the best way to achieve precise and reliable estimates. The objective of our study was to determine carbon in various components (leaves, branches, stems, structural roots and soil) of single-species plantations of *Vochysia guatemalensis* and *Hieronyma alchorneoides* from 0 to 16 years of age. Carbon fraction in the biomass, mean (\pm standard deviation), for the different pools varied between 38.5 and 49.7% (± 3 and 3.8). Accumulated carbon in the biomass increased with the plantation age, with mean annual increments of 7.1 and 5.3 Mg ha⁻¹ year⁻¹ for forest plantations of *V. guatemalensis* and *H. alchorneoides*, respectively. At all ages, 66.3% (± 10.6) of total biomass was found within the aboveground tree components, while 18.6% (± 20.9) was found in structural roots. The soil (0–30 cm) contained 62.2 (± 13) and 71.5% (± 17.1) of the total carbon (biomass plus soil) under *V. guatemalensis* and *H. alchorneoides*, respectively. Mean annual increment for carbon in the soil was 1.7 and 1.3 Mg ha⁻¹ year⁻¹ in *V. guatemalensis* and *H. alchorneoides*. Allometric equations were constructed to estimate total biomass and carbon in the biomass which had an R^2_{aj} (adjusted R square) greater than 94.5%. Finally, we compare our results to those that could have resulted from the use of default values, showing how site and species specific data contribute to the overall goal of improving carbon estimates and providing a more reliable account of the mitigation potential of forestry activities on climate change.

Keywords Allometric equations · Biomass expansion factor · Carbon fraction · Native tree plantations · Soil

W. Fonseca (✉) · F. E. Alice
Escuela de Ciencias Ambientales, Universidad Nacional de Costa Rica, Campus Omar Dengo,
86-3000 Heredia, Costa Rica
e-mail: wfonseca@una.ac.cr

J. M. Rey-Benayas
Departamento de Ecología, Universidad de Alcalá, Madrid, Spain

Introduction

After a long discussion on the contribution of forest ecosystems to the global carbon cycle, it seems as if these will finally be recognized through a Reduced Emissions from Deforestation and Degradation (REDD) mechanism, not only for their ability to absorb anthropogenic carbon but its function as a carbon reservoir. Both these functions have been estimated globally in the absorption of approximately 3 Pg C year⁻¹ (3 billion tons year⁻¹) through net growth (30% of CO₂ emissions from fossil fuel and deforestation) and the storage of an amount of carbon greater than that found in the atmosphere (Canadell and Raupach 2008).

Forest tree plantations have only had a small contribution to the total balance of terrestrial carbon (3.8% or 140 million ha of the world's total forest area; FAO 2006) but their potential to absorb and store carbon has been recognized to play a more important role in the future mitigation of climate change (Canadell et al. 2007). Besides, if forestry plantations are designed as elements within broader land management plans, they could be compatible with adaptation measures (Canadell et al. 2004; IPCC 2007; Paquette and Messier 2010) while overcoming some of the shortcomings discussed on some of the social and environmental benefits associated to these type of ecosystems (Bodegom et al. 2008; Paquette and Messier 2010), specially through native forest tree plantations (Montagnini et al. 2003; Jackson et al. 2005; Turner et al. 2005; Bodegom et al. 2008). However, scientific information that allows for the precise assessment of all these benefits and therefore the development of adequate policies is far from being complete (IPCC 2007; Nabuurs et al. 2007).

Many authors agree on the weaknesses from current estimates on the absorption and storage capacity of forest ecosystems (Elias and Potvin 2003; Chave et al. 2004; Sarmiento et al. 2005) and the implications these have on the development of climate change related policies (Ito et al. 2008; Somogyi et al. 2008). Such is the case of a future REDD mechanism or any other results-based payment scheme. In order to have a just distribution on the costs and benefits from these type of schemes, local, national or regional monitoring, reporting and verification systems with a higher degree of confidence in the estimates on the changes in carbon stocks is required (UNFCCC 2010). This leads to the need for site and species specific data, since 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 CO₂ ha⁻¹ year⁻¹; IPCC 2007; Sarmiento et al. 2005; Keith et al. 2009) are not being reflected under current estimates. These, are in most cases, currently 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.

Attempting to make a small but important contribution to the understanding of tropical forest ecosystems and as a means towards more precise and reliable estimates, this work provides exhaustive information for two native tree species (*V. guatemalensis* and *H. alchorneoides*) under forest plantations in humid tropical ecosystems in the Costa Rican Caribbean Region. These species were selected since they are the most promising native species in terms of productivity (Montero and Montagnini 2006; Piotto et al. 2010; Redondo 2007) and therefore the most commonly planted in the region. These have been used for construction or, in the case of *V. guatemalensis*, as wood pallets for shipping. Due to the combination of these factors, there has been an important advance in terms of the knowledge on these species including genetic improvement programs to improve their productivity and wood quality (Solís and Moya 2004a, b; Montero et al. 2007).

While trying to increase the precision and reliability of carbon estimates at a regional scale, we would also expect that the availability of such information might increase the consideration of the mitigation potential of these activities into forest policymaking. The objectives for this work were (1) to estimate the amount of accumulated biomass and carbon captured by single-species forestry plantations of two native species, at different ages, as well as its distribution in the different pools (biomass and soil); (2) to determine the biomass expansion factor for both species; (3) to determine the carbon fraction in the biomass for all the different components; and (4) to develop biomass models based on allometric relations to estimate biomass and carbon at the tree and ecosystem level.

Materials and methods

Study site and sample size

This study was conducted in the Costa Rican Caribbean region, corresponding to the very humid tropical forest life zone (Holdridge 1967). The altitude varies between 50 and 350 m asl. The climate is humid to very humid, hot to very hot, with or without a dry season of less than 25 intermittent days with water deficit per year (Herrera 1985; Mena 2009). The mean annual precipitation varies between 3,420 and 6,840 mm and mean annual temperature between 25 and 27°C. Soils are Ultisols, with less than 35% base saturation, deep, well drained, red or yellow in color and with a relatively low fertility (ITCR 2004).

A total of nine sites with forest plantations of *H. alchorneoides* and *V. guatemalensis* established in local farmers lands, were selected. In general terms, these plantations were established in lands where the previous land use was abandoned pastures, with relatively compacted soils and medium fertility. Distance between trees when planting took place was 3×3 for both species, although when sampling units were established, these plantations showed different distances due to age and management practices such as clearing and thinning. In each plantation of a given age, between one to eight sampling plots were established depending on the size of the plantation. The sampling units were rectangular with an area of 500 m². A total of 58 sampling plots were established in forest plantations of *H. alchorneoides* and 54 in *V. guatemalensis*. Plantation ages ranged from 0.5 to 16 years.

Biomass estimation

The estimates for the biomass and stored carbon followed the methods proposed by MacDicken (1997) with some modifications. A nested plot design was used, measuring the various biomass components (trees, herbs and necromass) in different sized subplots. For each of the biomass components that are described below, an approximately one kg field sub-sample was taken to the laboratory for analyses.

Aboveground tree biomass

In each 500 m² sampling plot, diameter at breast height (dbh) was measured for every tree and the tree with average dbh was selected and harvested for biomass measurements. A total of 54 trees with diameters between 0.5 and 40.5 cm were harvested in *V. guatemalensis* and 58 for *H. alchorneoides* with diameters between 0.5 and 28.8 cm. To quantify

biomass, a direct destructive sampling method was used, separating leaves, branches, stem and root components. For trees that due to their size represented an income for the plantation owner, to calculate their biomass we determined merchantable volume through the formula by Smalian (Prodan et al. 1997) and used the reported wood specific weight (Carpio 1995; CATIE 2003).

Belowground tree biomass

Belowground biomass refers exclusively to structural or coarse roots (and all of the fine roots attached to the main root after harvesting) from planted 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.

Biomass in herbaceous vegetation, small woody material and seedlings

Grasses, lianas, ferns, shrubs and some tree seedlings from natural regeneration with a dbh <2.5 cm, were measured in 1 × 1 m subplots located in every corner of the main 500 m² plot. In each 1 m² subplot all plant material was harvested to ground level and weighed in the field.

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 ≥2 cm in diameter). Fine necromass was estimated from four 0.5 × 0.5 m subplots (grouping these 4 subplots into one sample for analysis), while large necromass was evaluated from one 5 × 5 m subplot, all distributed randomly throughout the 500 m² plot. The collected material was then weighed in the field.

Soil organic carbon

The amount of carbon stored per hectare was obtained considering soil depth (cm), bulk density (g cm⁻²) and the percentage of soil organic carbon content (SOC). The sampling depth to determine carbon content was 30 cm, based on findings that support that as much as 60% of stored carbon has been found at this depth (Russell et al. 2007; Schedlbauer and Kavanagh 2008) and that at lower depths, stored carbon tends more stable (Sombroek et al. 1993) since the soil is less altered by mechanization practices or by changes in forest cover. Bulk density was determined through the cylinder method (MacDicken 1997), collecting one cylinder per plot. To determine SOC, a total of four soil samples were randomly selected within the main plot, extracted and mixed together in order to obtain a sample of approximately 1 kg. Sampling size were 58 for *H. alchorneoides* and 54 for *V. guatemalensis*.

Carbon fraction analysis in plant material and soil

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.).

Biomass expansion factor (BEF)

The biomass expansion factor is used to expand from a certain amount of tree volume or biomass, which includes some, but not all tree compartments, to another one that includes more or all tree compartments (Somogyi et al. 2008). In this case is the ratio between total aboveground biomass and stem, to be applied to transform stem volume into total aboveground biomass (Loguercio and Defossé 2001; Segura and Kanninen 2002; Dauber et al. 2008).

Biomass allometric models selection

The models were adjusted using the method of ordinary least squares. Methods presented by Salas (2002) and Segura and Andrade (2008) were followed to determine the best fit equation.

Mean annual increment (MAI)

This was expressed on the basis of both biomass (B) and carbon (C) per number of years (t), B/t and C/t, in Mg/ha (Prodan et al. 1997).

Results

Biomass and carbon accumulation

At ages 0.5, when most of the biomass was herbaceous vegetation, the amount of carbon in the total biomass was 1.1 and 0.9 Mg ha⁻¹ in *V. guatemalensis* and *H. alchorneoides* respectively. It then increased to 97.3 Mg ha⁻¹ in *V. guatemalensis* and 78.7 Mg ha⁻¹ in *H. alchorneoides*, by 16 years of age (Tables 1, 2). Averaged across 16 years, the MAI for total biomass and carbon in the total biomass were 14.5 and 7.1 Mg ha⁻¹ for *V. guatemalensis* and 10.0 and 5.3 Mg ha⁻¹ for *H. alchorneoides*. For carbon in the aboveground tree biomass, these were 4.2 and 3.0 Mg ha⁻¹ year⁻¹ for *V. guatemalensis* and *H. alchorneoides*, respectively. There was a positive correlation between carbon in the biomass and age for *V. guatemalensis* ($r = 0.79$, $P < 0.01$, $n = 56$) and for *H. alchorneoides* ($r = 0.63$, $P < 0.01$, $n = 61$).

From the total tree biomass, stems of *V. guatemalensis* and *H. alchorneoides* represent 62.0 and 55.6% respectively, followed by coarse roots (22.6 and 22.8%, respectively) and branches (11.7 and 17.5%, respectively). Leaves represented just a marginal proportion from total tree carbon (Table 1, 2). At an ecosystem level (total biomass) for both species, trees account for approximately 85%, while necromass (large and fine) contains about 12.5%. There was a negative correlation between the ratio of aboveground and belowground biomass related to plantation age ($r = -0.39$, $P = 0.01$, $n = 53$ for *V. guatemalensis* and $r = -0.32$, $P = 0.05$, $n = 58$ for *H. alchorneoides*).

Table 1 Biomass and carbon accumulation (Mg ha^{-1}) in *V. guatemalensis* single species forestry plantations

Pool	Components	Age (years)													
		0	0.7	3.2	5	7	9	12	14	16					
Tree B	Leaves		0.2 ± 0.2	3.5 ± 4.0	5.2 ± 0.4	4.5 ± 2.8	3.0 ± 1.4	6.4 ± 2.5	3.8 ± 1.8	5.1 ± 0.0					
	Branches		0.1 ± 0.1	5.3 ± 7.0	8.7 ± 2.7	12.2 ± 7.5	12.4 ± 8.7	39.9 ± 29.7	13.4 ± 8.4	8.8 ± 0.0					
	Stems		0.5 ± 0.1	8.9 ± 11.8	40.4 ± 7.6	60.2 ± 22.6	83.0 ± 30.0	113.6 ± 32.7	109.7 ± 69.0	145.5 ± 0.0					
	Roots		0.1 ± 0.0	4.8 ± 6.0	13.6 ± 2.0	21.9 ± 18.9	34.2 ± 16.8	33.5 ± 21.4	31.9 ± 19.6	52.6 ± 0.0					
	Total tree		0.5 ± 0.35	19.2 ± 27.4	68.6 ± 8.0	98.8 ± 39.1	132.5 ± 50.7	193.3 ± 81.2	157.8 ± 93.9	212.1 ± 0.0					
Tree C	Leaves		0.1 ± 0.1	2.2 ± 3.3	2.2 ± 0.3	1.9 ± 1.2	1.3 ± 0.5	2.7 ± 1.1	1.5 ± 0.7	2.0 ± 0.0					
	Branches		0.0 ± 0.0	3.1 ± 4.2	3.9 ± 1.3	5.8 ± 3.4	5.8 ± 4.0	18.6 ± 13.8	5.6 ± 3.9	3.4 ± 0.0					
	Stems		0.1 ± 0.0	5.0 ± 6.2	20.0 ± 1.2	28.8 ± 10.8	40.2 ± 14.4	54.8 ± 15.8	49.3 ± 30.5	64.2 ± 0.0					
	Roots		0.0 ± 0.0	2.9 ± 3.8	6.3 ± 0.9	10.2 ± 7.7	17.0 ± 8.0	16.4 ± 10.4	15.3 ± 9.6	25.6 ± 0.0					
	Total tree		0.24 ± 0.2	9.9 ± 13.3	32.3 ± 1.3	46.7 ± 16.9	63.9 ± 24.1	92.4 ± 38.7	71.7 ± 42.3	95.2 ± 0.0					
Herbaceous C		1.1 ± 0.1	0.3 ± 0.2	0.6 ± 0.4	0.6 ± 0.6	0.7 ± 0.5	0.6 ± 0.8	3.8 ± 0.0	0.2 ± 0.0						
Necromass C	Fine		0.0 ± 0.0	1.9 ± 1.4	2.1 ± 1.3	2.0 ± 1.1	1.6 ± 0.7	2.7 ± 1.1	2.7 ± 0.0	0.6 ± 0.0					
	Large		0.0 ± 0.0	0.0 ± 0.0	1.4 ± 0.1	3.1 ± 2.4	12.1 ± 21.7	2.4 ± 0.9	3.4 ± 0.0	1.2 ± 0.0					
Soil C			116.4 ± 51.0	85.8 ± 18.8	109.3 ± 13.6	116.3 ± 22.8	95.3 ± 38.9	127.5 ± 66.9	177.8 ± 30.9	87.0 ± 0.0					

Average ± SD

Table 2 Biomass and carbon accumulation (Mg ha^{-1}) in *H. alchorneoides* single species forestry plantations

Pool	Components	Age (years)									
		0	0.8	3.2	5	7.2	9.06	12	14.7	16	
Tree B	Leaves		0.3 ± 0.3	5.6 ± 3.2	1.7 ± 1.7	3.6 ± 0.7	3.8 ± 1.7	2.9 ± 0.8	3.7 ± 1.4	3.0 ± 0.5	
	Branches		0.1 ± 0.1	10.6 ± 8.4	2.3 ± 1.8	12.0 ± 10.1	23.7 ± 13.3	25.9 ± 7.3	13.8 ± 8.0	19.6 ± 4.7	
	Stems		0.5 ± 0.6	18.0 ± 13.3	7.2 ± 5.4	32.7 ± 13.0	55.8 ± 33.2	66.5 ± 12.6	68.5 ± 28.8	115.3 ± 22.8	
	Roots		0.2 ± 0.3	10.6 ± 7.6	3.8 ± 4.2	13.0 ± 8.7	27.7 ± 11.7	29.9 ± 5.3	29.3 ± 9.1	9.6 ± 19.1	
	Total tree		1.2 ± 1.3	44.7 ± 32.3	14.9 ± 12.7	61.3 ± 28.6	111.1 ± 51.5	125.1 ± 13.9	115.3 ± 40.7	146.5 ± 23.5	
Tree C	Leaves		0.1 ± 0.1	2.6 ± 1.4	0.7 ± 0.7	1.8 ± 0.3	1.7 ± 0.8	1.3 ± 0.3	1.7 ± 0.7	1.4 ± 0.2	
	Branches		0.1 ± 0.1	5.1 ± 4.0	1.2 ± 0.9	5.7 ± 4.8	11.8 ± 6.8	12.5 ± 3.5	5.9 ± 4.3	8.7 ± 1.8	
	Stems		0.3 ± 0.3	8.9 ± 6.6	3.7 ± 2.5	14.5 ± 6.2	28.0 ± 16.7	33.1 ± 6.2	34.1 ± 14.3	53.4 ± 8.8	
	Roots		0.1 ± 0.2	5.2 ± 3.8	1.7 ± 1.7	7.0 ± 4.3	13.3 ± 5.6	14.6 ± 2.6	14.3 ± 4.5	4.7 ± 9.4	
	Total tree		0.6 ± 0.6	21.8 ± 15.7	7.4 ± 5.6	29.0 ± 14.7	54.8 ± 25.7	61.6 ± 6.9	56.1 ± 19.1	68.3 ± 11.0	
Herbaceous C		0.91 ± 0.3	1.4 ± 0.6	0.7 ± 0.6	1.0 ± 0.4	1.0 ± 0.5	0.6 ± 0.4	0.2 ± 0.1	0.6 ± 0.4	0.1 ± 0.0	
Necromass C	Fine		0.0 ± 0.0	0.2 ± 0.7	3.4 ± 2.6	1.9 ± 2.0	2.2 ± 1.0	2.1 ± 0.7	5.1 ± 2.0	3.3 ± 2.3	1.2 ± 0.0
	Large		0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.5 ± 1.2	1.6 ± 1.4	4.9 ± 7.2	1.6 ± 0.9	2.3 ± 4.1	0.9 ± 0.0
Soil C		124.9 ± 63.6	77.2 ± 19.3	76.7 ± 16.1	73.0 ± 41.2	111.3 ± 17.9	98.5 ± 37.2	177.9 ± 21.0	109.8 ± 27.5	101.8 ± 0.0	

Average ± SD

Carbon accumulated in the soil (at 30 cm depth) in the period from 0.5 to 16 years of age went from 85.8 to 107.0 Mg ha⁻¹ in *V. guatemalensis* (± 46.5 and 14.1) and 77.2–101.8 Mg ha⁻¹ (± 45.0 and 21.8) in *H. alchorneoides*. The average for all MAI values for the different ages in the carbon found at the soil was 1.7 and 1.3 Mg ha⁻¹ year⁻¹ respectively. Changes observed for carbon in the soil were statistically significant and the correlation between soil carbon and plantations age was positive but low ($r = 0.38$, $P = 0.01$, $n = 56$ for *V. guatemalensis* and $r = 0.36$, $P = 0.01$, $n = 61$ for *H. alchorneoides*).

The amount of total carbon (biomass and soil) went from 88.7 Mg ha⁻¹ at early ages (when 98.9% is soil carbon) to 204.3 Mg ha⁻¹ at 16 years (when 52.4% is soil carbon) in *V. guatemalensis* forest plantations. For *H. alchorneoides* these results were 79.4 Mg ha⁻¹ in recently established plantations (when 99.7% is soil carbon) and 180.48 Mg ha⁻¹ at 16 years (when 56.4% is soil carbon). Soil carbon had a negative correlation with the age of the stand ($r = -0.68$, $P < 0.01$, $n = 56$ for *V. guatemalensis* and $r = -0.62$, $P < 0.01$, $n = 61$ for *H. alchorneoides*). The total amount of carbon stored in the soil averaged 62.2 and 71.5% in *V. guatemalensis* and *H. alchorneoides*, respectively, with average MAI for total carbon of each of the different ages evaluated in forest plantations of *V. guatemalensis* of 8.7 and 6.5 Mg C ha⁻¹ in *H. alchorneoides*.

Carbon fraction in the biomass

The carbon fraction for the more lignified biomass components (stem, branches, roots and large necromass) in plantations of 0.5–16 years, varied between 46.5 (± 4.7) and 48.6% (± 3.7) in *V. guatemalensis* tree plantations and between 47 (± 9.9) and 49.7% (± 3.8) in *H. alchorneoides* (Table 3). The carbon fraction for leaves, herbaceous vegetation and fine necromass (litter) from these plantations varied between 38.5 (± 2.9) and 44.6% (± 3.3) in *V. guatemalensis* and between 42.8 (± 9.1) and 45.9% (± 4.7) in *H. alchorneoides*. The standard deviations were below five, except for branches, herbaceous vegetation and fine necromass of *H. alchorneoides* (Table 3).

Biomass expansion factor (BEF)

The BEF for *V. guatemalensis* was 1.56 (± 0.72) and 1.57 (± 0.42) for *H. alchorneoides*.

Table 3 Carbon fraction (%) in the biomass of forest tree plantations with ages between 0.5 and 16 years

Species	Statistics	Stem	Branches	Leaves	Roots	Herbaceous vegetation	Large necromass	Fine necromass
<i>V. guatemalensis</i>	<i>X</i>	48.11	46.46	42.95	48.63	44.64	48.51	38.50
	<i>SD</i>	4.11	4.73	3.85	3.68	3.26	4.57	2.97
	<i>n</i>	59	59	59	59	68	41	44
<i>H. alchorneoides</i>	<i>X</i>	49.67	47.65	45.94	49.24	43.99	46.98	42.79
	<i>SD</i>	3.77	7.99	4.74	3.39	21.25	9.9	9.11
	<i>n</i>	61	60	61	58	72	45	51

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

Table 4 Selected model for the estimation of total biomass and carbon in the biomass (Mg ha^{-1}) in forestry plantations of *V. guatemalensis* and *H. alchorneoides*. All models with $P < 0.0001$

Species	Selected model	R^2_{aj} (%)	SEE	IF	n
<i>V. guatemalensis</i>	$\text{Log}(\text{BT}) = 1.32107 + 0.678129 * \sqrt{G}$	95.3	0.381	1.28	64
	$\text{Cba} = (0.146365 + 1.38023 * \sqrt{G})^2$	96.6	0.657		56
	$\text{Log}(\text{CBT}) = 0.540135 + 0.68418 * \sqrt{G}$	94.6	0.413	0.73	64
<i>H. alchorneoides</i>	$\text{BT} = \exp(0.891012 + 1.08278 * \sqrt{G})$	96.4	0.333		65
	$\text{Log}(\text{Cba}) = -1.42086 + 1.51576 * \sqrt{G}$	96.0	0.406	1.27	51
	$\text{CBT} = \exp(0.0934072 + 1.11676 * \sqrt{G})$	96.4	0.345		65

G basal area in $\text{m}^2 \text{ha}^{-1}$, BT total biomass in Mg ha^{-1} , Cba carbon in tree biomass Mg ha^{-1} , CBT carbon in total biomass in Mg ha^{-1} , R^2_{aj} adjusted coefficient of determination, SEE model's standard error, IF furnival index, n sample size, \exp natural log base = 2.718271

Allometric models for the estimation of biomass and carbon

The selected allometric models to estimate total biomass and carbon in plant material (planted trees, herbaceous vegetation and necromass) resulted in adjusted R^2 greater than 94.5%; all models were significant ($P < 0.01$), had low standard errors (Table 4) and showed a normal distribution. The models with the better adjustment express the logarithmic transformation of the dependent variable as a square root function of the basal area.

Discussion

Carbon accumulation in forest tree plantations

Despite differences in methodologies and environmental conditions, other tree plantations in Costa Rica have reported similar C accumulation rates to those obtained through this study ($4.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in *V. guatemalensis* and $3.0 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in *H. alchorneoides*). For native species such as *Bombacopsis quinata*, *Terminalia amazonia*, *V. guatemalensis*, *Dipteryx panamensis*, *H. alchorneoides* and *Virola koschnyi* results have been reported between $1.7\text{--}7 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (Cubero and Rojas 1999; Montero and Kanninen 2002; Pérez and Kanninen 2003; Redondo and Montagnini 2006; Redondo 2007). In exotic tree species, *Tectona grandis* and *Gmelina arborea*, reported results are in the range of $2.0\text{--}6.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (Cubero and Rojas 1999; Subak 2000; Pérez and Kanninen 2003). However, these estimates do not take into account components such as roots, herbaceous vegetation or necromass, which, as shown by our results, cause significant increases in MAI ($7.1 \text{ Mg ha}^{-1} \text{ year}^{-1}$ for *V. guatemalensis* and $5.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in *H. alchorneoides*).

In this study, the differences in biomass and carbon accumulation between both species were largely due to differences in their growth rates (Redondo 2007). *V. guatemalensis* has a fast growth rate and a short rotation period close to 15 years (Petit and Montagnini 2004; Solís and Moya 2004b), while *H. alchorneoides* has a lower growth rate and rotation periods between 25 and 40 years (Solís and Moya 2004a, b; Montero et al. 2007).

Annual carbon accumulation rates in the soil from this study, 1.7 Mg ha^{-1} in forest plantations of *V. guatemalensis* and 1.3 Mg ha^{-1} in *H. alchorneoides*, are above MAI values of 0.66 Mg ha^{-1} in forestry plantations (Russell et al. 2007) and similar to 1.9 for

secondary forests in Ecuador (Rhoades et al. 2000). However, SOC estimates in tropical forest ecosystems, where carbon content is highly variable according to spatial distribution, makes comparisons as well as precise measurements and extrapolations quite difficult (Mendoza et al. 2003; Bauhus et al. 2005; Jandl 2006).

Although most studies agree that the soil is the most important carbon pool in forest ecosystems (Russell et al. 2007; Schedlbauer and Kavanagh 2008; Solís and Moya 2004b; Tschakert et al. 2007), changes in carbon stocks within this pool are not easy to assess. Changes observed were statistically significant, although the positive but low correlation between soil carbon and age, suggests a low enhancement of soil carbon due to forest tree plantations. These results could be explained due to the young age of the studied plantations and the slow carbon incorporation to the soils reported by other studies (Singh et al. 2007; Gamboa et al. 2008). However, previous land use might be also playing an important role. Guo and Gifford (2002) cited by the IPCC (2007) report that sites with low initial soil carbon stocks such as those after prolonged cultivations, increase carbon content after reforestation, while it might decrease after reforestation occurs on sites with high soil carbon contents such as grasslands. Although some studies agree with these losses, these have been reported to recover after several years (Gaboury et al. 2009; Tan et al. 2009). Similar to our results, significant net changes after the transition from pasture lands to secondary forests have been reported (Veldkamp et al. 2003; Powers and Veldkamp 2005; Schedlbauer and Kavanagh 2008) but in different age forest fallows, other studies have failed to find significant differences among different age groups (Tschakert et al. 2007). All these results reveal that there is not a common trend, or at least not one that can be easily discerned from our results, and that most probably carbon accumulation in the soil responds to a combination of circumstances that include everything from previous land use, site specific conditions (Schöning et al. 2006) and the land cover being evaluated. Therefore, identifying consistent changes in the carbon stock from soils seems to require site specific measurement and extrapolations should be avoided.

Biomass carbon fraction

A carbon fraction of 0.5 has been recognized as an acceptable average, therefore being the most common conversion factor used (Hoen and Solberg 1994; Husch 2001; Losi et al. 2003; Sarmiento et al. 2005; Montero and Montagnini 2006; Redondo 2007). However, studies have also shown that the use of carbon fractions in the range of 0.45 and 0.50 might account for as much as a 10% difference when applied to the same site and the same set of data (Elias and Potvin 2003). Based on our biomass data and comparing both the obtained carbon fraction and the lower end value from the accepted range (0.45), we determined underestimations in total tree biomass between 4 and 6% depending on specie due to the use of 0.45.

Overestimations are still more common when considering components less lignified such as fine necromass, tree leaves and herbaceous vegetation. For these, as results from this study show and which are supported by Gifford (2000); Gayoso and Guerra (2005) and Sarmiento et al. (2005), carbon fractions are in the range of 0.40 and 0.45. Therefore, extrapolating on the assumption that all plant biomass has a constant carbon fraction will only lead to increased errors.

Biomass expansion factor (BEF)

BEF determined for both species in this study (1.56) is within the lower end of the range reported for different species in tropical natural forests and forest plantations (1.5–2.88)

(Soliz 1998; Segura et al. 2000; Arreaga 2002; Montero and Kanninen 2002; Dauber et al. 2008; Fonseca et al. 2009). Using a 1.75 BEF recommended by Brown and Lugo (1989) and cited by Chacón et al. (2009) as an appropriate average used in the Costa Rican National Greenhouse Gas Inventory, we estimated an average of 29% more carbon when applied to our total tree biomass data (27.7 and 20.8 Mg C ha⁻¹ for *V. guatemalensis* and *H. alchorneoides*, respectively).

Carbon distribution in the biomass compartments

In this study, with the exemption of herbaceous vegetation and necromass, the compartments that account for the greatest amount of carbon in the ecosystem were estimated with acceptable sampling errors (between 10 and 15% which are within the levels proposed by MacDicken 1997).

The fact that the stem accounts for the largest amount of carbon from total tree biomass has been largely documented, with ranges going from 50 to 92% for different species from forest plantations (Gutiérrez and Lopera 2001; Pérez and Kanninen 2003; Redondo 2007; Redondo and Montagnini 2006). Although our results are within this range (62 and 55.6% for *V. guatemalensis* and *H. alchorneoides* respectively), these are found within the lower end of the reported range considering that we included coarse roots in our estimations.

Coarse roots accumulate the largest amount of belowground carbon but are almost unknown for most tropical tree species (MacDicken 1997; Sarmiento et al. 2005). When using the average percentage of coarse roots in total tree biomass for both species estimated in this study (22%), an increase of 18.8 Mg C ha⁻¹ would be obtained if compared to the 10–15% recommended by MacDicken (1997) as a conservative estimate. This result agrees with Sarmiento et al. (2005), who state that most estimates from this component are most probably underestimations.

At an ecosystem level, necromass and herbaceous vegetation are also usually neglected in most studies (Chave et al. 2004; Sarmiento et al. 2005). These represented in our study almost 15% from the total carbon in the biomass, evidencing the importance of such pools for carbon accounting. These pools also play an important role for their contribution to soil fertility and degraded land restoration processes (Fisher 1995; Montagnini and Mendelsohn 1997; Montagnini 2000).

Allometric models

The selection of the equation to be used for the estimation of biomass and carbon has been regarded as the most important source of error (Chave et al. 2004; Návár 2009), with overestimations as high as 100% due to the use of generic equations (van Noordwijk et al. 2002). Common errors when selecting an equation occur when using these for zones different from those where it was developed (Buvaneswaran et al. 2006) or for diameter ranges outside the one used in their construction (Losi et al. 2003; Chave et al. 2004; Sarmiento et al. 2005). These same authors mention that when constructing an equation, weaknesses are usually related to a small sample size and failing to take into account wood specific gravity.

Published allometric models for individual tropical trees (Pérez and Kanninen 2002; Montero and Montagnini 2006; Návár 2009), rarely include the amount of carbon corresponding to coarse roots or the amount of biomass and carbon per hectare from other biomass compartments. The presented models were developed including all compartments,

based on a large set of samples ($n > 50$) and in the case of tree biomass, on a large range of diameters and ages, and achieving a good prediction capacity ($>94.5\%$ in all cases).

Conclusions

Carbon in the biomass was over 78 Mg/ha but the soil represents the main carbon sink at an ecosystem level with more than 85 Mg/ha. Mean annual increments for carbon in the biomass was above 5.3 Mg/ha and over 1.3 Mg/ha in the soil. The stem represents the most important component from tree biomass with carbon MAI values above 3 Mg/ha.

Considering that the development of local biomass equations is a resource expensive operation, models that allow per hectare quantification of biomass and carbon using simple field estimation variables such as basal area represents an important advantage towards the precise and reliable quantification of carbon accumulation in these plantations. However, we agree with most authors, in cautioning that the use of these equations should be preceded by a thorough review of their applicability to the studied community in order to avoid over or underestimations.

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