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Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama

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Abstract

Reforestation is being considered as a mitigation option to reduce the increase in atmospheric carbon dioxide and predicted climate change. Forestry-based carbon storage projects are being introduced in many tropical countries, and assessment of carbon storage potentials is made difficult by a lack of species-level information. We measured above- and belowground biomass and tissue carbon content of 20-year-old teak (*Tectona grandis*) trees in four Panamanian plantations to estimate carbon storage potential. A regression relating diameter at breast height (DBH) to total tree carbon storage was constructed and used to estimate plantation-level tree carbon storage, which averaged 120 t/ha. Litter, undergrowth and soil compartments were estimated to contain 3.4, 2.6 and 225 t C/ha, respectively. The soil carbon was a one-time measurement, not an estimate of soil C accumulation. We estimate carbon storage in Panamanian harvest-age teak plantations to be 351 t C/ha. Various methods of calculation of carbon storage in short-rotation plantations are discussed.

Résumé

Hoy en día, la reforestación está siendo considerada como una opción para mitigar los cambios climáticos predichos como resultado de la contaminación atmosférica por dióxido de carbono. En muchos países tropicales se están introduciendo proyectos forestales de almecenaje de carbono. Este estudio se enfoca en la teca (*Tectona grandis*) para medir varias características que afectan el potencial de almacenaje de carbono tanto de los árboles como de las plantaciones donde se encuentran. Se midieron la proporción raíz-vástago, la biomasa total y el contenido de carbono en los tejidos en árboles de teca de veinte años de edad en plantaciones panameñas. Se desarolló una regresión que relaciona el diámetro a la altura del pecho con la cantidad total de carbono en el árbol que fue utilizada para estimar la cantidad de carbono almacenada en los árboles de cuatro plantaciones. Encontramos un promedio de 120 t C/ha en los arboles. Se estudiaron la hojarasca. el sotobosque, y los perfiles de los suelos, y encontramos promedios de 3.4, 2.6 y 225 t C/ha en esos compartimentos, respectivamente. Estimamos un almacenaje de carbono de 351 t/ha por estas plantaciones. Se discuten varios métodos de cálculo del almacenaje de carbono en plantaciones de rotación corta.

Keywords: Forestry; Carbon dioxide mitigation; Root biomass; Allometric equations; Soil carbon

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1. Introduction

Of the 130 million ha of forest plantations in the world (Allan and Lanly, 1991), just over half are located in the tropics (FAO, 1995). The total carbon storage that can be credited to global forest plantations today is an estimated 11.8 Pg C (Winjum and Schroeder, 1997), about 10% of the carbon lost through land conversion since industrialization. Forestry activity designed to store carbon is often proposed for the tropics, as tropical climates support rapid vegetation growth rates (Schroeder and Ladd, 1991). Marland (1998) estimated that based on higher potential growth rates, the area required to capture annual carbon emissions could be reduced by 25% if afforestation efforts were centred in the tropics. Grainger (1988) calculated that the tropics contain 758 million ha of depleted or degraded lands which were once forested. Reforestation of these areas would capture significant amounts of atmospheric carbon, and would be expected to contribute to soil quality and conservation (Schroeder, 1992). Although there are several estimates of carbon storage in various forest types (Brown, 1993; Lugo and Brown, 1992; Vogt, 1991), few estimates of individual species' carbon storage potential have been published. To allow informed choices between species when establishing carbon storage projects, it is important to characterize various traits which influence carbon storage on a per species basis. Such information would also be useful for inclusion in global carbon storage/cycling models.

For most species used for reforestation, only aboveground biomass potentials are known. To have a whole picture of species' carbon storage potential, one must know aboveground-to-belowground biomass allocation patterns. Belowground allocation of biomass in forests ranges widely, e.g., in tropical dry forests the contribution of roots to total biomass has been estimated to range from 18 to 46% (Sanford and Cuevas, 1996).

This study was conducted in Panama, where forestry plantation is rapidly increasing in popularity. From 1992 to 1998, the area of abandoned land that had been reforested rose from 11 000 to 34 600 ha. Just over half of these reforestation projects have been conducted using teak (ANAM, 1999a). Today, teak ranks third among tropical hardwood species in terms of plantation area established world-wide, covering 2.25 million ha (Krishnapillay, 2000). It is planted extensively in the world's tropics for high-quality timber. Because of teak's increasing popularity as a plantation species, we chose to study its carbon storage potential. Schroeder and Ladd (1991) point out the importance of considering a species' cumulative carbon storage potential rather than its potential maximum growth rate at some point during its lifecycle when estimating its carbon storage potential. For this reason, this work was conducted in plantations of harvest-age, which for teak in Central America is 20 years.

The goals of this work were: (1) to measure teak root-to-shoot ratio, total biomass and tissue carbon concentrations, as well as litter production, undergrowth biomass and carbon storage, and soil carbon storage in teak plantations, (2) to develop two non-destructive predictors of teak tree carbon storage and biomass (one for whole trees, the other for the root compartment), and (3) to produce an estimate of the carbon storage potential of Panamanian teak plantations at harvest age. The tree carbon measured in this work represents the carbon sequestered by a plantation over its lifetime. To translate this to carbon storage potential, it is necessary to include information about the harvest and replanting of such a plantation. A discussion of the possible methods of calculation of carbon storage of these plantations follows.

2. Materials and methods

2.1. Study site

This study was conducted in four 20-year-old teak plantations in Panama's Canal Zone (9°20′N, 79°50′W), established by Panama's National Authority for the Environment (ANAM) in 1978–1979. Three of the plantations are on Lago Alajuela in Chagres National Park (Boquerón, Peñas Blancas and Tranquilla), the other is in Soberanía National Park (Aguas Claras), all within 25 km of each other, inside the watershed of the Panama Canal. These are small-scale plantations of about 5 ha each, and have received very little management, with only natural thinning and no undergrowth removal. Basic characteristics of the trees of these plantations are listed in Table 1. Common

Table 1
Basic characteristics of the study plantations (trees, $n = 48$ per plantation)[a]

Plantation name	Average tree density (per ha)	Average DBH (cm)	Average tree height (m)	Tree species composition (teak:palm:other)
Boquerón	586	23.7 (7.6) ab	20.7 (4.1)	98:0:2
Peñas Blancas	566	26.6 (8.6) a	19.6 (4.4)	96:1:3
Tranquilla	621	25.3 (6.7) ab	20.6 (4.3)	90:8:3
Aguas Claras	723	21.9 (5.0) b	20.6 (4.2)	93:1:6
Average	624	24.4	20.4	94:3:3

[a] Letters denote groups of significantly similar DBH, based on ANOVA analysis ($\alpha = 0.05$). Standard deviations in parentheses.

undergrowth species are *Gustavia superba*, *Heliconia latispatha*, *Andira inermis* and *Bactris* sp.

Average daily temperatures in this zone range between 23 and 30 °C, and annual precipitation varies between 2300 and 3000 mm, with a 4-month-long dry season from December to April (ANAM, 1999b). The soils of these plantations were derived from sedimentary rocks of tertiary age (Weyl, 1980), and soil textures tend to be loamy throughout the profile (Table 2).

2.2. Scales of study

To investigate the carbon storage in these plantations, we worked on two different scales: the tree level and the plantation level. We measured tree tissue biomass and carbon concentration to describe the relationship between DBH and carbon storage of individual trees. At the plantation level, the tree-based work was scaled up to estimate the amount of carbon stored in the trees of the plantations, using average DBH and tree density for each plantation. This was supplemented by litter, undergrowth and soil carbon mass estimates.

Average and range of tree size were estimated using the 48 trees closest to two 100 m transects established at right angles to each other in each plantation. DBH and height were measured using diameter tape and a clinometer (Haga). From these 192 (4×48) trees, nine trees covering the range of size present in the four plantations were subsampled to be harvested for above- and belowground measurement of biomass and tissue carbon concentrations. At each plantation except Tranquilla (where the lack of water supply precluded root harvest), the 48 trees were separated into three groups of 16 based on size, and from each size class one tree was randomly selected for harvest.

Felling areas were cleared of litter and undergrowth and the trees were directionally felled. Aboveground biomass was separated into different tissue types (large, medium, small leaves, flowers, twigs, and branches), and the trunk cut up into metre-long pieces.

Table 2
Basic characteristics of the study plantations (soil, with pH and bulk density of surface samples (0–10 cm depth, $n = 15$ per plantation), and colour of dry soil according to Munsell soil colour charts; surface layer = 0–10 cm depth, bottom layers = 10 cm to bottom of pit)

Plantation name	Soil texture	Soil colour	Average profile depth (cm)	Bulk density (g/cm^3)	pH
Boquerón	Surface layer: silty loam Bottom layer: loam	Light grey 2.5 years (7/2)	180	0.63 (0.07)	6.6 (0.7)
Peñas Blancas	Surface layer: loam Bottom layer: clayey loam	Reddish-yellow 5 years (6/6)	>200	0.74 (0.10)	6.2 (0.2)
Tranquilla	Surface layer: loam Bottom layer: loam	Brownish-yellow 10 years (6/6)	160	0.75 (0.13)	5.9 (0.3)
Aguas Claras	Surface layer: slightly clayey loam Bottom layer: slightly clayey loam	Dark yellowish-brown 10 years (4/4)	190	0.66 (0.20)	6.1 (0.4)

To excavate the coarse roots (>5 mm in diameter), we started at the stump and followed the roots to their ends. For the most part their growth was shallow and lateral, without a taproot. As the tree density was high, it was difficult to distinguish between fine root systems of different trees sharing the space. To deal with this problem, pits were established around each tree as the coarse roots were excavated, from which all soil was removed to isolate the fine roots. The soil was manually washed using a low-pressure water source over a 1 cm mesh. The perimeters of these pits were set halfway between the focal trees and their neighbours (an average of 1.5 m from the focal tree). Outside of these pits no fine roots were collected, to balance for the foreign fine roots which were collected from within the pit. In this study, fine roots were considered to be <5 mm in diameter. The technique of washing the soil did not allow us to collect all fine roots present. To estimate the amount of fine roots of diameter smaller than 5 mm not collected, 12 trials were performed at each tree. Five litres of soil from random areas in the pit were processed as normal, then the washed soil was collected and all fine roots it contained possible to collect by hand were isolated from it. To calculate the proportion of roots left behind by our >5 mm technique, we compared the total fine root masses collected in the trials to the fine root masses collected as usual. This average proportion was added to each tree's fine root mass. We believe this accounted for most of the roots not measured by our collection method. No attempt was made to separate dead and live roots in either size class.

Wet masses of all materials were measured using a Viking 300 lb capacity spring scale (Viking). Samples were immediately taken from each tissue type to obtain wet-to-dry mass conversions and for later carbon content analysis. The tree-specific wet-to-dry mass conversion factors for different tissues were used to convert total wet mass per tissue to total dry mass per tissue for each tree. These dry masses were then converted to tissue carbon storage by multiplying them by tree- and tissue-specific carbon concentrations.

Plantation-level work was performed in all four study plantations. Tree density in these plantations was estimated by counting all trees in a random area of 25×25 m^2. The litter layer (any dead plant material on the plantation floor) was collected at the end of the dry season (1999). The accumulated mass of litter was used to approximate the annual litter fall. On average, the woody portion made up 17% of the litter. We do not know what part of this portion of the litter came from the current year or from previous years. Teak and non-teak litter were separately collected from 12 randomly located 1×1 m^2 plots. Aboveground biomass of non-teak undergrowth was collected from five 3×3 m^2 plots in each plantation at the end of the wet season (1999). Because we were only able to sample aboveground undergrowth, total undergrowth biomass was estimated from measured aboveground biomass by multiplication by 1.34, based on the root-to-shoot ratio for tropical deciduous forest plants reported by Jackson et al. (1996).

Fifteen random soil samples were taken from the soil surface (0–10 cm) of each plantation. As well, samples were taken at each 10 cm of depth from two or three 2 m deep pits in each plantation. Soil profile depth was measured as the average depth at which each plantation's pits became rocky and resistant to sampling. Bulk density, pH, soil texture and organic matter content were measured for both surface and pit samples.

2.3. Sample treatment and chemical analysis

The sealed tree tissue samples and collected litter and undergrowth were weighed wet within 3 days of being collected, using a Salter-AND-EK scale with 12 kg capacity (Salter). They were dried at 70 °C for 1 week, and reweighed to produce tissue-specific wet-to-dry mass conversion factors.

To prepare for organic carbon determination, the vegetation samples were ground with mortar and pestle using liquid nitrogen. For each of the nine study trees, all samples per tissue type were pooled into one 100 g sample. Subsamples of 100 g in size were taken from the material from eight randomly chosen litter samples per plantation. Within each subsample, teak and non-teak litter were recombined in their original mass proportion. Dry material from each of the five undergrowth plots was chopped into fine pieces, subsampled, ground, and for each plot a subsample of 100 g in size was taken for carbon determination. These subsamples were analysed for carbon concentration using gas chromatography on a CHN Elemental Analyser, EA 1108 (Fisons Instruments). The analyser was monitored for accuracy of readings every 10 samples with a sulphanilamide standard.

The soil samples were dried for 1 week at 70 °C, and sieved using 2 mm mesh to remove any vegetation or gravel present. Soil texture was estimated manually, as described by Schlichting et al. (1995). Acidity (pH) was measured in 0.01 M calcium chloride in a ratio of 1:3, using an Orion Research Digital Ionalyzer, Model 601 (Orion Research). Organic matter content of all soil samples was estimated through loss on ignition (LOI), by combustion in a muffle furnace at 350 °C for 16 h (Hesse, 1971). CHN analysis (as done on the vegetation samples) was performed on 30 of these samples to provide organic carbon content. These data were used to build a regression between organic carbon content and LOI. The relationship was statistically significant ($p < 0.0001$), had a coefficient of determination of 0.715, and the standard error of estimate was 1.044. This regression was applied to the other soil samples to estimate their organic carbon content.

Soil data were grouped into various layers of depth in all profiles. Average bulk density, organic carbon concentration and organic carbon storage were calculated for these profile layers (Fig. 2).

2.4. Statistical analysis

Various linear regressions were constructed using DBH as the independent variable, and total tree biomass, total tree carbon storage, root biomass and carbon storage as dependent variables, using data from all nine trees. All these data were transformed using log to the base 10, as is commonly done to linearize data of this type. One-way analysis of variance was used to test the differences between carbon contents of the various tree tissues. As well, tissues were grouped as woody (trunk, branches, coarse roots and twigs) and soft (leaves, flowers and fine roots), and the difference in carbon content between these groups was tested using one-way analysis of variance. One-way analyses of variance were also used to test whether pH, root-to-shoot ratios, mass and carbon concentrations of litter and undergrowth, undergrowth-to-teak litter ratios, tree height and DBH varied among plantations. Two-way analysis of variance was used to test whether bulk density and % soil carbon varied among plantations and depths. All statistical analyses were conducted using Systat 9.0 for Windows.

3. Results

Average tree heights range between 19.6 and 20.7 m, and average DBH ranges from 21.9 to 26.6 cm (Table 1). Analysis of variance showed that the trees at Aguas Claras had a smaller average DBH than the trees of Peñas Blancas ($F = 3.84$, $p = 0.011$).

3.1. Biomass and carbon concentration of teak tissues

While values of DBH of the nine excavated trees ranged between 16.9 and 43.8 cm, total tree dry biomass varied from 122 to 1365 kg. On average, woody tissues (trunk, branches, twigs and coarse roots) made up 95% of a tree's mass (Table 3). These woody tissues have significantly higher carbon concentrations than the soft tissues: leaves, flowers and fine roots (49.2 and 46.4%, respectively, $F = 120$, $p < 0.0001$). By weighting the carbon concentrations of the different tissue types by the proportion of the total tree biomass they represent, we obtain an average of teak tree carbon concentration (49.5%) which can be used to obtain tree carbon storage estimates using total tree biomass. The carbon storage of the nine harvested trees ranges from 60 to 674 kg.

Simple linear regressions of log DBH versus log - dry biomass, and log DBH versus log carbon storage show that these relationships are strong, yielding coefficients of determination (r^2) of 0.978 for both regressions (Fig. 1). The linear regression of DBH versus root system biomass and carbon storage (Fig. 1) shows that 87% of the variation in root biomass and carbon in a teak plantation can be explained by DBH of the trees.

3.2. Root-to-shoot ratio

Root-to-shoot ratios (R:S) ranged from 0.11 to 0.23 in the nine excavated trees, with a mean of 0.16. When carbon concentrations of these tissues are taken into account, on average 13.1% of the trees' carbon was stored in their roots, and 86.9% in their shoots. Variability in root-to-shoot ratio was not strongly related to tree size. Linear regression was not used to analyse these data due to a violation of standard assumptions which could not be remedied by transformation.

Table 3
Proportion of tissue types in terms of biomass and tissue-specific carbon concentrations[a]

Tissue type	Proportion of total tree biomass (%)	Tissue carbon concentration (%)
Small leaves (<25 cm long × 15 cm wide)	0.28	46.4 (1.1) abg
Medium leaves ((35 × 20)–(25 × 15) cm^2)	0.83	46.5 (0.9) abg
Large leaves (>35 cm × 25 cm)	1.90	47.0 (0.8) ab
Flowers (from six trees)	0.26	47.2 (0.4) ab
Twigs	1.28	47.2 (0.4) ab
Branches	16.76	48.7 (0.6) cdf
Upper trunk (upper third)	14.43	49.6 (0.9) cdef
Mid-trunk (middle third)	19.43	50.2 (0.4) de
Lower trunk (lower third)	31.42	50.4 (0.8) de
Coarse roots (>5 mm diameter)	11.65	48.8 (0.6) cdf
Fine roots (<5 mm diameter)	1.76	45.2 (1.1) ag

[a] In all tissue categories 10 samples per tree were taken, except for the trunk categories, where five samples per tree were taken. Biomass proportion values are averages over nine trees. Carbon concentration values are averages of pooled samples from nine trees. Letters denote groups of significantly similar tissue carbon concentrations, based on ANOVA analysis ($\alpha = 0.05$). Standard deviations are in parentheses.

Instead, the Pearson correlation coefficient was computed to measure the strength of association between the two variables. Its value was −0.292, revealing a weak negative association between DBH and root-to-shoot ratio which was statistically insignificant. One-way ANOVA showed that plantation identity did not affect tree root-to-shoot ratio significantly ($F = 0.62$, $p = 0.571$).

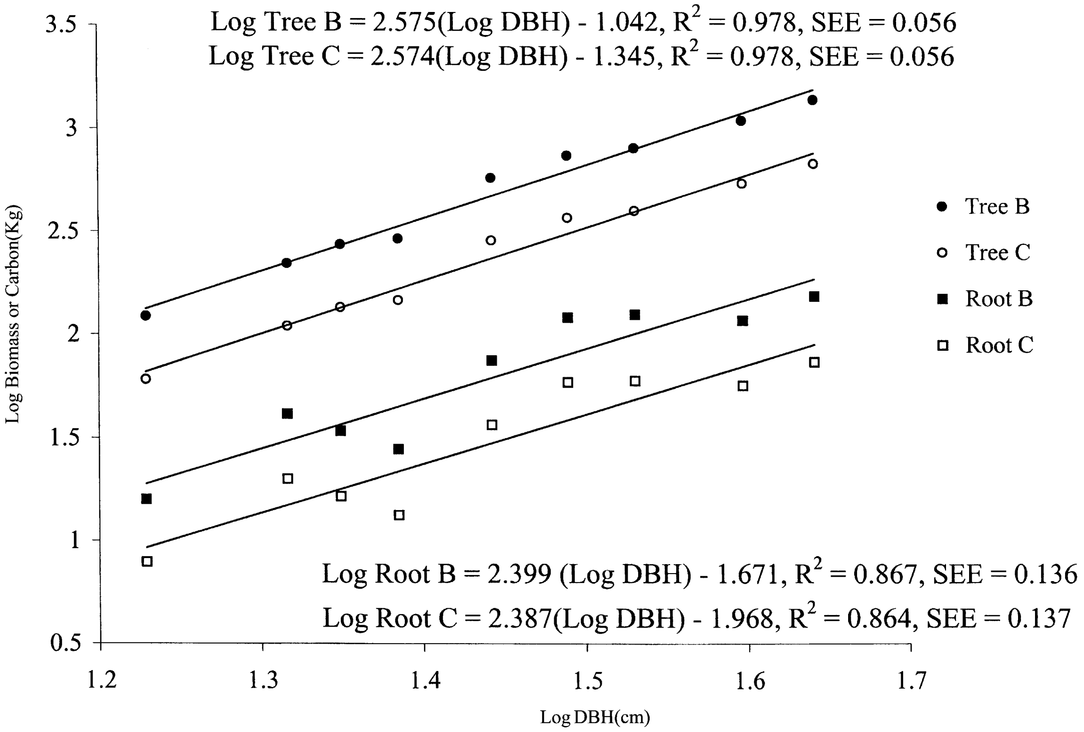

Fig. 1. Linear regressions of DBH versus total tree dry biomass (●), total tree carbon storage (○), root system dry biomass (■) and root system carbon storage (□), for the nine study trees (all data log-transformed).

Table 4
Vegetation carbon storage values at the plantation level (tree carbon storage)

	Carbon storage per tree (kg)	Underground tree carbon storage (t/ha)	Aboveground tree carbon storage (t/ha)	Total tree carbon storage (t/ha)
Boquerón	180	13.8	91.8	105.6
Peñas Blancas	248	18.4	122.2	140.6
Tranquilla	217	17.6	117.1	134.8
Aguas Claras	138	13.1	86.8	99.8
Average	196	15.7	104.5	120.2

3.3. Plantation-level carbon storage

The largest tree carbon storage at the plantation level was found at Peñas Blancas (141 t/ha), while the smallest was found at the Aguas Claras plantation (100 t/ha) (Table 4). The mean carbon storage in tree roots of the plantations is 15.7 t/ha, while the mean shoot carbon storage is 104.5 t/ha. The mean total tree carbon storage at the plantation level is 120.2 t/ha (Table 4, Fig. 3).

There was no significant difference between the biomass and carbon concentrations of undergrowth collected in the four different plantations ($F = 0.56$, $p = 0.684$). The average carbon concentration of the undergrowth is 44.4%, about 2% smaller than the carbon concentration of yearly cycling teak tissues, 46.4% ($F = 27.92$, $p < 0.0001$), both inputs to the plantations' litter. Average undergrowth biomass was calculated to be 5.8 t/ha, containing 2.6 t carbon/ha (Table 5, Fig. 3).

No significant difference was found between the mean amounts of litter collected in the four different plantations ($F = 0.56$, $p = 0.642$, Table 5). Average dry mass of litter which accumulated over the dry season in these plantations was 7.9 t/ha, containing 3.4 t C/ha (Table 5, Fig. 3). On average, litter collected was made up of 7% undergrowth tissue, and 93% teak tissue. Averages of the undergrowth-to-teak ratio of litter mass were found to be significantly different between plantations ($F = 3.52$, $p = 0.030$). The mean carbon concentration of the litter was 43.3%, and did not vary significantly between plantations ($F = 1.48$, $p = 0.242$; Table 5).

The textures and colours of the soils differed between plantations, reflecting differences in parent material (Table 2). The surface soil at Boquerón was found to be significantly less acidic than the surface soil of the other plantations ($F = 7.0$, $p < 0.0001$). No difference was found when comparing the average surface soil (0–10 cm) bulk densities of the four plantations, which ranged between 0.63 and 0.75 g/cm^3. There were insignificant differences between plantations in terms of average profile bulk density. A significant difference was found in soil organic carbon concentration among plantations ($F = 7.98$, $p < 0.001$). Both carbon concentration and bulk density changed significantly with depth ($F = 12.78$, $p < 0.001$ and $F = 6.37$, $p < 0.001$, respectively),

Table 5
Vegetation carbon storage values at the plantation level (litter and undergrowth carbon storage)[a]

	Mass (t/ha)		Carbon concentration (%)		Carbon storage (t/ha)	
	Litter	Undergrowth	Litter	Undergrowth	Litter	Undergrowth
Boquerón	8.4 a (3.2)	4.9 a (4.7)	42.3 a (1.4)	45.7 a (1.3)	3.6	2.2
Peñas Blancas	7.7 a (1.5)	6.6 a (4.0)	43.1 a (2.6)	43.9 a (2.7)	3.3	2.9
Tranquilla	7.3 a (3.8)	4.19 a (2.9)	43.9 a (1.3)	43.8 a (0.8)	3.2	1.8
Aguas claras	7.9 a (3.1)	7.5 a (6.1)	43.8 a (1.2)	44.1 a (1.6)	3.5	3.3
Average	7.9	5.8	43.3	44.4	3.4	2.6

[a] Undergrowth plots per plantation: $n = 5$, litter plots per plantation; biomass: $n = 24$; carbon concentration: $n = 8$. Letters denote groups of significantly similar mass or carbon concentration values, based on ANOVA analysis ($\alpha = 0.05$). Standard deviations in parentheses.

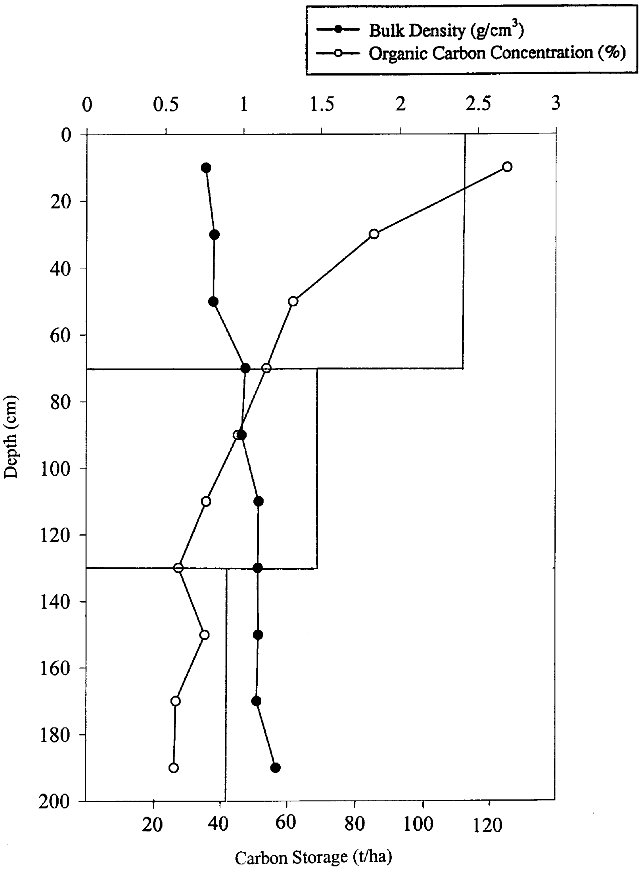

Fig. 2. General patterns of bulk density and organic carbon concentration as affected by depth. Bars denote carbon storage per depth increment. Values are averages over the four study plantations.

and the interaction between plantation and depth had significant effect in the case of carbon concentration ($F = 1.70$, $p = 0.044$). The bulk density and carbon concentrations of the various soil samples combined across plantations give a general picture of carbon storage at different depths (Fig. 2). Carbon concentration decreased with depth in a general pattern of exponential decay.

4. Discussion

Fig. 3 summarizes the knowledge we have about the carbon storage in this system. The largest new carbon store, after the establishment of the plantations, is the trees themselves. Average carbon storage in the trees of these mature plantations is 120 t/ha. As much of the trees' carbon is located aboveground, the longevity of this carbon store depends on the fate of this wood once it has been harvested. The litter and undergrowth of this system contain a moderate amount of carbon when compared to the other compartments (Fig. 3). Adding carbon stored in undergrowth and litter (2.6 and 3.4 t C/ha, respectively) to the plantation estimate, the carbon storage figure rises to 126 t/ha. The figure shows that most of the carbon in the system is in the soil, averaging 225 t/ha, bringing the total carbon in each hectare of these plantations to 351 t.

The strength of the regression relating DBH to tree carbon storage allows confident use of the equation for estimation of carbon stores in trees of harvest-age teak plantations. This tool may prove useful both for application in existing plantations, as well as for prediction of potential carbon storage when combined

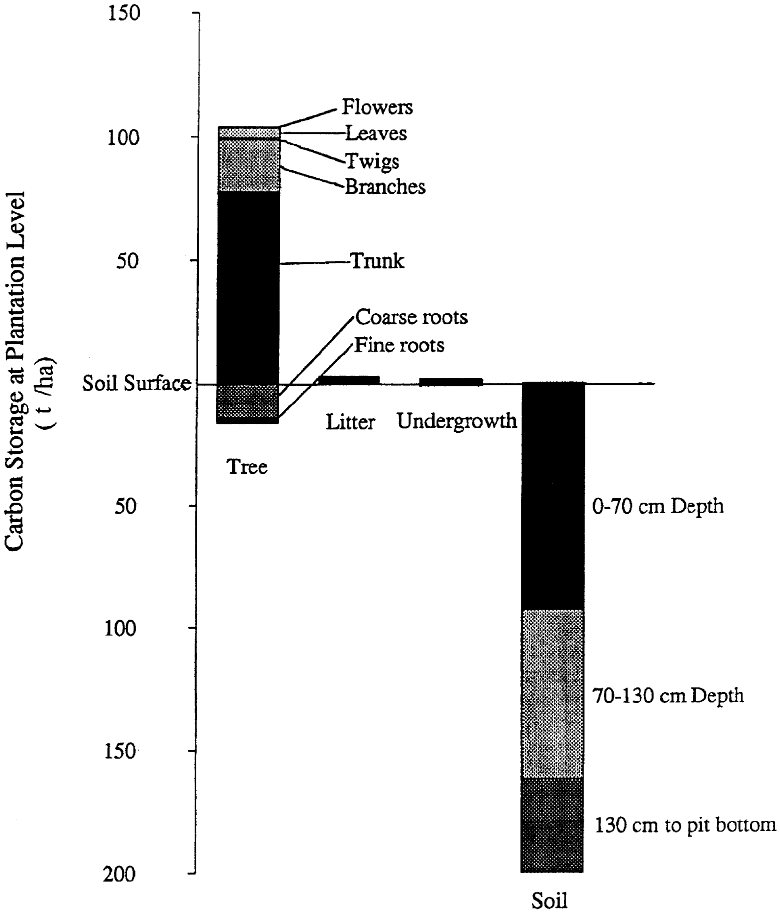

Fig. 3. Carbon storage in various compartments at the plantation level. Storage values below the soil surface line represent belowground carbon stores. Values are averages over the four study plantations.

with site-index curves which predict productivity of various sites in terms of tree size. The regression which predicts biomass and carbon storage of tree roots allows accounting of a carbon store until now unknown in size. Since the plantations studied in this work were not thinned, the equations presented here would have decreased accuracy in managed plantations if R:S were affected by management treatments.

The amount of carbon stored in a tree's roots is often substantial, but is unknown for many species. Despite teak's increasing popularity as a tropical reforestation species, little work had yet been done investigating the species' complete biomass (Karmacharya and Singh, 1992). We found only one article which addressed teak's belowground biomass allocation (Hase and Foelster, 1983), a study performed in Venezuela in an age series of teak plantations up to 9 years. Comparing our root-to-shoot results with those of Hase and Foelster, there is a progressive decrease in the values of this ratio with increasing plantation age, from 0.42 at 4 years to 0.20 at 9 years, to our result, 0.16 at 20 years of age. The fact that we found no relationship between root-to-shoot ratio and tree size (DBH) in this study suggests that this trend may be linked more directly to development with age than tree size.

The mean root-to-shoot ratio found in these teak plantations is small as compared to the more general ratio that Cairns et al. (1997) produced from a review of tropical forest biomass studies. They found the average R:S for primary and secondary tropical forests was 0.24. The amount of root carbon storage and transmission of carbon to the soil through the roots may be lower in forest plantations as compared to natural forests. Cuevas et al. (1991) studied a *Pinus caribaea* plantation and secondary forest of the same age, growing in the same climate and on the same soils in Puerto Rico. Total biomass was similar in the two systems, but the pine plantation allocated only 6% of total production belowground to roots, whereas the secondary forest allocated 44% of its production belowground.

In breaking up the tissues and determining separate carbon concentrations for each tissue type, a pattern of decreasing carbon concentration toward the trees' extremities was revealed. The biomass-weighted mean carbon concentration was 49.5%, very close to the 50% value often used for estimation of carbon storage from dry biomass information. The biomass and carbon which turned over yearly in the trees of the study plantations was small relative to their total biomass. These biomass compartments made up 5% of the trees' total biomass at 20 years of age, while long-lived, woody tissues made up 95% of the biomass. Karmacharya and Singh (1992) investigated primary production allocation in the trees of an age series of teak plantations in Kerala, India, and found that in later stages of development, though the more ephemeral tissues make up a small part of the trees' total standing biomass, the trees have shifted much of their production toward these tissues. At 30 years of age, 50% of the trees' production went into woody parts, and 50% into softer-tissue parts which turn over rapidly. In the Panamanian study trees, when considering total production over a tree's lifespan, the ephemeral tissues take on much greater importance. Though not storing carbon within the tree itself for long, they fall as litter, which can channel the portion of carbon not decayed directly to the atmosphere toward the soil carbon pool.

The litter accumulated on the floors of these plantations was comparable in quantity to the annual litterfall of surrounding forest (Table 5). Leigh and Windsor (1982) found that in the forest of BCI, less than 50 km away from the furthest of the study plantations, litterfall was 6.1 t/(ha per year), and state that litterfall in most lowland tropical forests ranges between 6 and 8 t/(ha per year). Measures in Sardinilla, a point central to the four plantations studied here, show that the litter quantity on their study pasture is 2.5 t/ha (Moore et al., submitted). The increase in litter from pasture to plantation is appreciable, but the gain in carbon storage in this compartment is small compared to the gain in the tree compartment.

4.1. Carbon storage of Panamanian teak plantations

The 120 t of carbon stored in the trees of 1 ha of these Panamanian teak plantations is similar to the final stocks of Australian radiata pine and Brazilian slash pine on medium site classes (171 t C/ha over 45-year rotation and 112 t C/ha over 30-year rotation, respectively), as estimated by Nabuurs and Mohren (1995). Cuevas and Medina (1986) published biomass figures for three types of Amazonian forest, estimated equivalent to 152 t C/ha in Terra Firme forest, 178 t C/ha in Tall Caatinga forest and 155 t C/ha in Tall Bana forest. The six Central American lowland tropical forest sites reported by Sanford and Cuevas (1996) contained an average of 146 t C/ha. Using this figure, we estimate that at the end of their rotation the teak plantations store about 85% the amount of carbon of the surrounding forest when unperturbed.

The carbon stored in these plantations may also be compared to carbon storage in the vegetation of pasture in Sardinilla, to quantify the increase in carbon storage which may accompany reforestation with teak. The grazed pasture of Sardinilla supported 2 kg C in a hectare of vegetation (Moore et al., submitted). This figure is expected to be higher on abandoned land.

4.2. Carbon storage calculations

The IPCC's default carbon storage calculation is based on the amount of carbon stored in the trees of a plantation at the end of their growth cycle (UNEP et al., 1995). This is not a serious source of error if the trees are not harvested until some long time after they reach maturity (Christie and Scholes, 1995). Teak, however, is grown for valuable hardwood, and in commercial plantations is cut upon reaching the desired size. As short-rotation plantations have high capacity for carbon sequestration but short-term capacity for carbon storage, their carbon storage potentials should be examined as mean storage over time, including harvest and regrowth, rather than as peak carbon contents just prior to harvest (Schroeder, 1992). Nabuurs and Mohren (1995) also underline the short-term nature of the short-rotation plantation carbon sink. They focus on long-term results by calculating carbon storage over many rotations.

Schroeder proposed a revised method for estimation of carbon storage by short-rotation plantations, representing the average tree carbon storage over many rotations. We used our data for teak to calculate long-term storage using this mean carbon storage method. To estimate standing crop for each year of the plantation, we used a growth curve of teak grown in Costa Rica in a GTZ project (COSEFORMA, 1998) to calculate what proportion of final yield had been reached at each year of growth. Our calculations with teak data resulted in a mean carbon storage estimate of 76 t C/ha.

Winjum and Schroeder (1997) used the mean carbon storage calculation to estimate the carbon storage capacity of various forest plantations, and concluded that storage in the phytomass of plantations generally increases from high to low latitudes, ranging from 47 to 81 t C/ha. Our mean storage estimate for Panamanian teak plantations falls into the upper part of this range.

Tree plantations also store carbon in products made from harvested wood, and this makes up an important part of their carbon storage potential. From our biomass data, we estimated that the study trees contained 60% of their biomass in usable trunk wood. This represents an average of 72 t C/ha in harvestable wood per rotation. The loss of teak biomass while sawing a trunk into lumber is 58% (Van den Ende, pers. comm.) leaving 30 t C/ha in sawed logs. Further losses would be sustained in transforming saw logs into finished products, depending on the product made. Winjum and Schroeder (1997) estimate that over a 50-year period, harvests from plantations in low latitudes store 15–37 t C/ha in wood products. Our above calculations show that over 50 years one would obtain 60 t C/ha in saw logs. By transformation into finished products, this may be reduced to an average in the range of Winjum and Schroeder's estimate, though decomposition of these products would have yet to be factored in to get an equilibrium storage value.

To recompare the carbon storage of the teak plantations to surrounding forest, taking a longer-term view, one can see that mean storage in the vegetation of the plantations is about one-half of the storage of the surrounding undisturbed forest (146 t C/ha, Sanford and Cuevas, 1996). Storage in wood products could make this gap considerably more narrow.

It is important to keep in mind that mean carbon storage values for plantations are only valid while the plantations exist and are replaced after each harvest. After the plantation is discontinued, the vegetation carbon storage on the land is much lower, akin to pasture values, though plantation sites may be left storing more carbon than before planting in cases where tree presence and management engendered soil rehabilitation and soil carbon storage. In contrast, forests store carbon for much longer time scales without need for human intervention. The plantation of trees whose ephemeral tissues (as opposed to their wood) are used as products may approach forest carbon sequestration capacity, as their mean carbon storage is not continually cut back by harvests of wood. As well, these plantations can support locals, and in doing so may help to slow surrounding deforestation.

The carbon stored in the first metre of the soil of these plantations is comparable to the expected amount of carbon in the first metre of tropical soils, 130–160 t/ha (Jobbágy and Jackson, 2000). Measurements taken in Sardinilla have shown that the establishment and growth of teak plantations to the age of 7–8 years provokes a very slight increase in soil carbon storage, amounting to less than 20 t/ha (Moore et al., submitted). From this observation, we assume that much of the carbon of the soils of our study plantations was present before the establishment of the plantations. Moore's data suggest that the plantation of abandoned land with teak does not promote significant increases in carbon storage in the soil as the plantation grows. An important question about the soil carbon storage potential of plantations is the size of the contribution of decomposing stumps and roots to soil carbon over many rotations. Greater addition of carbon to the soil compartment may be achieved by planting more deeply rooted tree species (Jobbágy and Jackson, 2000).

5. Conclusion

From our calculations, we conclude that teak plantations have appreciable mean carbon storage capacity, much greater than that of the abandoned pasture they were planted on. The compartment of the plantation with the greatest potential for carbon sequestration and storage is the wood biomass (120 t C/ha). The litter and undergrowth together contribute only about 6 t C/ha per year. The total potential storage of teak plantations is considerable, but not as large and long-lasting as those of surrounding natural forest or of plantations established for the collection of ephemeral tissues.

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