# Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species

**Marlène Elias and Catherine Potvin**

**Abstract:** Trunk carbon (C) concentrations were assessed for 32 species of tropical trees to understand sources of variation. The main effect of species accounted for 38% of the total variance in C concentration ($p < 0.0001$). *Tectona grandis* demonstrated the greatest C concentration (49.4%), while *Ormosia macrocalyx* displayed the lowest C concentration (44.4%). We also observed significant differences among the sampling sites ($F = 2.2$, $p < 0.02$). For three of the species sampled in both plantations and natural forests, the natural forest individuals had significantly higher C concentrations (*Dipteryx panamensis*: $F = 6.10$, $p = 0.06$; *Hura crepitans*: $F = 5.53$, $p = 0.06$; and *Miconia argentea*: $F = 8.92$, $p = 0.02$). C concentration was highly correlated with wood specific gravity ($r^2 = 0.86$). A canonical correspondence analysis was performed to identify the environmental and (or) growth factors explaining variation in trunk C concentration. The two factors with the highest loading values on the first canonical axis are site and diameter at breast height (DBH), while DBH and density load on axis 2. The biplot shows that species respond differently to environmental factors. Our results suggest that a better consideration of interspecific variation in C concentration could reduce the error associated with estimates of C sequestration by up to 10%.

**Résumé :** La concentration de carbone (C) dans le tronc de 32 espèces d'arbres tropicaux a été déterminée pour connaître les sources de variation. L'effet principal dû à l'espèce comptait pour 38 % de la variation totale de la concentration de C ($p < 0,0001$). *Tectona grandis* avait la plus forte concentration de C (49,4 %) tandis que *Ormosia macrocalyx* avait la plus faible (44,4 %). Nous avons également observé des différences significatives entre les sites d'échantillonnage ($F = 2,2$, $p < 0,02$). Pour trois des espèces échantillonnées tant en plantation qu'en forêt naturelle, les individus échantillonnés en forêt naturelle avaient une concentration de C significativement plus élevée (*Dipteryx panamensis*: $F = 6,10$, $p < 0,06$; *Hura crepitans*: $F = 5,53$, $p < 0,06$; *Miconia argentea*: $F = 8,92$, $p < 0,02$). La concentration de C est étroitement corrélée avec la masse spécifique du bois ($r^2 = 0,86$). Une analyse canonique des correspondances a été effectuée pour identifier les facteurs environnementaux et de croissance qui expliquent la variation dans la concentration de C dans le tronc. Les deux facteurs ayant la plus forte valeur sur le premier axe canonique sont le site et le diamètre à hauteur de poitrine (DBH) tandis que le DBH et la masse spécifique ressortent sur le deuxième axe. Le diagramme de double projection montre que les espèces réagissent différemment aux facteurs environnementaux. Nos résultats indiquent que l'erreur associée aux estimations de séquestration du C pourrait être réduite jusqu'à 10 % en prenant en considération la variation interspécifique dans la concentration de C.

[Traduit par la Rédaction]

## Introduction

Rapid postindustrialization increases in the atmospheric $CO_2$ concentration have prompted numerous studies on the global carbon (C) balance (e.g., Brown and Lugo 1982; Dixon et al. 1994; Canadell and Pataki 2002). Forest ecosystems have been estimated to store approximately 60% of terrestrial C (Winjum et al. 1992), with roughly 40% of global C biomass being in the tropics and subtropics (Brown and Lugo 1982). To estimate C storage, land-use areas need to be converted into biomass estimates using allometric equations. Much attention has recently been given to the improvement of these equations (Chave et al. 2001; Ketterings et al. 2001; Nascimento and Laurance 2002). Few articles, however, have considered the relative potential and contribution of different species in forest C cycling and sequestration (Lugo et al. 1990; Bassow and Bazzaz 1997). Standard approximation for tree C content is to multiply biomass by 0.50 (W. Laurance, personal communication). The lack of quantitative data on C sinks and C densities for the various components of tropical forests has been pointed out as a knowledge gap of concern (e.g., Kraenzel et al. 2003; Lugo 1992; Delaney et al. 1997).

The aim of this study is thus to investigate interspecific variations in trunk C concentration among 32 species of tropical trees. We also examined variation between ecological groups and sampling sites, as well as the importance of tree size and environment (e.g., canopy closure) on %C. This should provide information on possible sources of vari-

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**Table 1.** Ecological characteristics for the sampling sites.

| Site[a] | No. of species | C concn. (%C) | DBH (cm) | Canopy closure[b] | Slope steepness[b] | Soil humidity[b] | Tree density[b] |
|---|---|---|---|---|---|---|---|
| 1[c] | 9 | 45.9 | 23.4 | 2.4 | 1.9 | 1 | 1.9 |
| 2 | 7 | 46.0 | 25.5 | 2.8 | 2.9 | 1.1 | 2.0 |
| 3 | 10 | 45.9 | 41.3 | 2 | 2.1 | 1.2 | 1.7 |
| 4 | 1 | 45.9 | 11.8 | 3 | 3.5 | 1 | 2.5 |
| 5 | 10 | 45.9 | 21.4 | 3.2 | 1.9 | 1 | 2.7 |
| 6[c] | 11 | 45.7 | 10.7 | 1.9 | 2.5 | 1.0 | 1.4 |
| 7 | 10 | 46.4 | 37.6 | 3.6 | 2.6 | 1.4 | 1.6 |
| 8 | 2 | 46.6 | 38.8 | 2.6 | 1.9 | 1.0 | 1.6 |
| 9 | 3 | 46.4 | 37.4 | 1.8 | 1.9 | 1 | 2 |
| 10 | 6 | 46.6 | 36.4 | 1.8 | 1.9 | 1 | 1.9 |
| 11 | 3 | 45.9 | 64.2 | 2.2 | 1.2 | 1 | 1 |

**Note:** Entries in the table are averages for all individuals sampled at a given site.
[a]1, Proyecto Agroforestal Rio Cabuya; 2, Soberania National Park Camino del Oleoducto; 3, Sardinilla; 4, Chagres National Park; 5, Soberania National Park Sendero la Bonga; 6, Las Pavas; 7, Barro Colorado Island; 8, Fort Sherman; 9, Parque Natural Metropolitano; 10, Ipeti-Embera; 11, Roadsides in the Canal area.
[b]Assessed using an arbitrary scale of 1–4.
[c]Plantation sites (Rio Cabuya (1) and Las Pavas (6)).

ation in trunk C concentration. Additionally, this paper examines the relationship between trunk C concentration and wood specific gravity, a trait that could be used as a surrogate for trunk C concentration. An understanding of the stability of trunk C concentration might be interesting in the management of forests and plantations toward C sequestration (e.g., Brown 1993; Houghton et al. 1991; Sedjo and Solomon 1989; Schroeder 1992; Winjum and Schroeder 1997; Vitousek 1991; Kraenzel et al. 2003). We contend that if we uncover high variation in C concentration, this trait should deserve increased attention in estimates of C sequestration of forests or plantations.

## Materials and methods

### Data collection

Thirty-two species of trees from 19 families were sampled from 11 sites located in central Panama during July and August of 1999. With the exception of teak, *Tectona grandis*, all species are native to Panama and have been described by Croat (1978). The sites included two plantations in the Panama Canal region and eight primary or secondary natural forests (Table 1). For prevalent species, individual trees were randomly selected from the 11 sites. Four to six individuals were sampled in forests and four to six others in plantations, whenever possible (Table 2). Rarer species were sampled without fail when encountered. Three species were not often encountered in forests or plantations (*Simarouba amara*, *Ormosia macrocalyx*, and *Tabebuia guayacan*). Additional samples were therefore taken from planted individuals along roadsides in the Canal area (site 11). Species choice rested on four criteria: (*i*) species with a known moderate to high growth rate on Barro Colorado Island (BCI); (*ii*) species commonly encountered in the sampling sites; (*iii*) species tagged by local farmers as useful for firewood or construction purposes; and (*iv*) species having a known market in Panama. Leaf specimens were brought to the Smithsonian Tropical Research Institute herbarium for confirmation of their taxonomy. Species were classified in ecologically distinct groups following discussions with S.P. Hubbell, University of Georgia, and R. Peres, Smithsonian Tropical Research Institute. The classification was determined largely by the occurrence of the species in the 50-ha permanent plot of BCI and is coherent with physiological characteristics (Ellis et al. 2000). Species classified as pioneers are encountered more frequently in gaps than in a closed forest. Other species, light intermediate and shade-tolerant, were classified as nonpioneers. Fifteen species were classified as pioneers and 17 as nonpioneers.

One trunk sample per individual was collected at breast height (1.3 m) with a 1 cm diameter wood corer, and diameter at breast height (DBH) was recorded. Four ecological characteristics of the surroundings of each individual tree were estimated: canopy closure, slope steepness, soil humidity, and tree density. Each variable was coded 1–4, ranging from low to high. The wood cores were oven-dried at the Smithsonian Tropical Research Institute. Tree cores were finely ground and analyzed at McGill University for C concentration (%) using an automated elemental analyzer (model EA 1108, FISONS Instruments, Milan, Italy). Internal standards were used to correct for possible variations of the instrument between runs. Duplicates of every sample were analyzed, and when their values differed by more than 5%, further samples were run. Wood specific gravity (SG) was determined by H. Muller-Landau, Princeton University (personal communication), from samples collected from fresh tree falls on BCI. Wood SG values were based on calculating fresh volume divided by ovendry mass of wood samples. Sampling was carried out during the rainy season of 1999 for a subset of nine species. The number of species included in the analysis of wood SG was limited by the number and identity of fresh tree falls encountered on the island.

### Data analysis

Interspecific variation in C concentration among the 32 species and among sites was analyzed with a two-way analysis of variance (ANOVA) with no interaction term. The spe-

**Table 2.** The 32 species in the study as classified in two ecological groups: pioneer (P) or nonpioneer (N).

| Scientific name | Code | Family | Group | $n^a$ |
|---|---|---|---|---|
| *Anacardium excelsum* | ANE | Anacardiaceae | P | 9 |
| *Antirrhoea trichantha* | ANT | Rubiaceae | P | 5 |
| *Bursera simaruba* | BUS | Burseraceae | N | 5 |
| *Cecropia insignis* | CEI | Moraceae | P | 5 |
| *Cecropia peltata* | CEP | Moraceae | P | 4 |
| *Cedrela odorata* | CEO | Meliaceae | N | 5 |
| *Cordia alliodora* | COA | Boraginaceae | P | 9 |
| *Croton draco* | CRD | Euphorbiaceae | P | 4 |
| *Dipteryx panamensis* | DIP | Leguminosae | N | 7 |
| *Enterolobium cyclocarpum* | ENC | Leguminosae | N | 9 |
| *Faramea occidentalis* | FAO | Rubiaceae | N | 5 |
| *Genipa americana* | GEA | Rubiaceae | N | 5 |
| *Gustavia superba* | GUS | Lecythidaceae | N | 5 |
| *Hampea appendiculata* | HAA | Malvaceae | P | 4 |
| *Hura crepitans* | HUC | Euphorbiaceae | N | 9 |
| *Luehea seemannii* | LUS | Tiliaceae | P | 6 |
| *Miconia argentea* | MIA | Melastomataceae | P | 9 |
| *Ochroma pyramidale* | OCP | Bombacaceae | P | 5 |
| *Ormosia macrocalyx* | ORM | Leguminosae | N | 6 |
| *Palicourea guianensis* | PAG | Rubiaceae | N | 5 |
| *Poulsenia armata* | POA | Moraceae | N | 7 |
| *Protium tenuifolium* | PRT | Burseraceae | N | 7 |
| *Simarouba amara* | SIA | Simaroubaceae | N | 4 |
| *Sterculia apetala* | STA | Sterculiaceae | P | 10 |
| *Swietania macrophylla* | SWM | Meliaceae | N | 8 |
| *Tabebuia guayacan* | TAG | Bignoniaceae | N | 11 |
| *Tabebuia rosea* | TAR | Bignoniaceae | N | 10 |
| *Tectona grandis* | TEG | Verbenaceae | P | 5 |
| *Trema micrantha* | TRM | Ulmaceae | P | 5 |
| *Trichilia tuberculata* | TRT | Meliaceae | N | 6 |
| *Zanthoxylum belizense* | ZAB | Rutaceae | P | 4 |
| *Zanthoxylum setulosum* | ZAS | Rutaceae | P | 6 |

[a]Number of individuals sampled from each species.

cies by site interaction was excluded because individual species were not present at all the sites. The magnitude of the two experimental effects, species and site, was estimated following Winer et al. (1991). Potential variation in C concentration according to ecological group (pioneer or nonpioneer) was analyzed in a second ANOVA using a nested design in which species were nested under ecological groups. The latter was considered a fixed effect.

The 11 sites in which trees were sampled were compared for DBH, canopy, slope, humidity, and density. ANOVA was used for analysis of DBH, while Kruskal–Wallis rank-sum test was preferred for the four categorical variables. For each of the 10 species sampled in both plantations and natural forests, the difference in C concentration between the two habitats was tested by one-way ANOVA. A canonical correspondence analysis (CCA) was performed to identify the environmental factors explaining variation in trunk C concentration. We used the forward selection option of the statistical package CANOCO, version 4.0, with 999 permutations (ter Braak and Smilauer 1998). Besides the five above-mentioned variables, we included sampling sites and habitats in the environmental matrix.

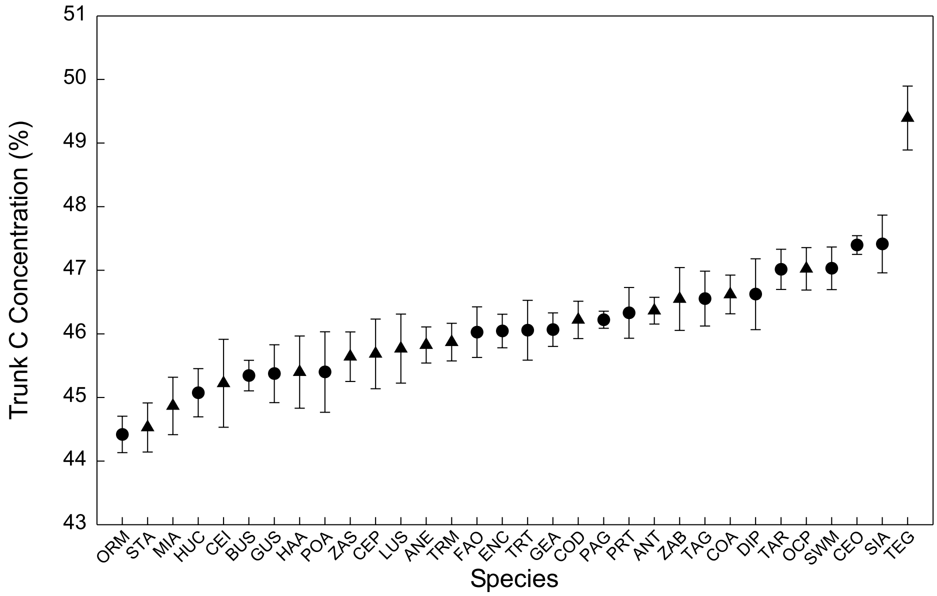
For nine species, the relationship between C concentration and wood SG was evaluated with regression analysis. The correlation between C concentration and tree diameter, both within and across species, was examined using Pearson's correlation coefficient. Data were analyzed with the SYSTAT 9.0 statistical package.

## Results

### Interspecific differences in C concentration

Species had significantly different trunk C concentrations ($F = 5.41$, $p < 0.0001$). The main effect of species accounted for 38.7% of the total variance in C concentration. Mean %C per species varied between 44.4 and 49.4%, with *Ormosia macrocalyx* and *Tectona grandis* flanking the lower and upper limits, respectively (Fig. 1). Individual tree values ranged between 42.3% (*Poulsenia armata*) and 51.1% (*Tectona grandis*). The three species with the lowest C concentration were *Ormosia macrocalyx*, *Sterculia apetela*, and *Miconia argentea*. Their C concentration differed significantly from those of the six species storing the greatest amount of %C, namely *Tabebuia rosea*, *Swietenia macro-*

**Fig. 1.** Trunk C concentration for the 32 species sampled. Each point is the mean per species, and vertical lines represent the standard error of the mean. Triangles correspond to pioneers and circles to nonpioneers. Species codes are defined in Table 2.




*phylla*, *Ochroma pyramidale*, *Cedrela odorata*, *Simarouba amara*, and *Tectona grandis* (Tukey matrix of pairwise probabilities, $p < 0.05$) (Fig. 1). In particular, teak distinguished itself from 29 of the 32 species studied with respect to its elevated C concentration ($p < 0.03$). Ecological grouping, conversely, was unsuccessful in explaining variations in C concentration ($F = 0.23$, $p = 0.63$). Average trunk C concentration for pioneer (45.9% ± 1.4) and nonpioneer (46.2% ± 1.3) species was very similar. There was significant variation among species within a group ($F = 5.18$, $p < 0.001$), confirming that species rather than ecological group determines C concentration.

### Environmentally induced variation in C concentration

The sampling sites were statistically different in DBH ($F = 8.45$, $p < 0.001$), canopy (Kruskal–Wallis = 48.5, $p < 0.0001$), slope (Kruskal–Wallis = 29.4, $p < 0.001$), humidity (Kruskal–Wallis = 29.04, $p < 0.001$), and density (Kruskal–Wallis = 37.45, $p < 0.001$) (Table 1). Trees sampled along roadsides had the highest average DBH. Pearson's correlation analyses failed to uncover a significant correlation between C concentration and DBH whether within or across species. In a two-way ANOVA combining species and site, site was found to exert a statistically significant effect on C concentration ($F = 2.20$, $p < 0.02$), accounting for 3.4% of the total variance. CCA was chosen to study the relationship between trunk C concentration of the 32 species and environmental variables of the individual trees. The only environmental factor not retained by the CCA was habitat (Fig. 2). The reduced model indicated that axis 1 accounted for 25.1% of the species by environment variance, while axis 2 explained an additional 22.1% of the variance. The two factors with the highest loading values on axis 1 were site (0.7604) and DBH (0.3907), while the main loading factors for axis 2 were DBH (0.4017) and density (–0.3848). The least important environmental factors were humidity followed by canopy. The CCA biplot showed that different species responded differently to the six environmental and (or) growth variables (Fig. 2). For some species, e.g., *Ormosia macrocalyx*, trunk C concentration increased with DBH, while for others, e.g., *Croton drago*, the reverse trend was observed. Similar species-specific variation in response to the various sampling sites was observed. In the biplot, nonpioneer species codes are in bold–italic. Visual examination failed to identify clustering of ecological groups in response to environmental and (or) growth variables.

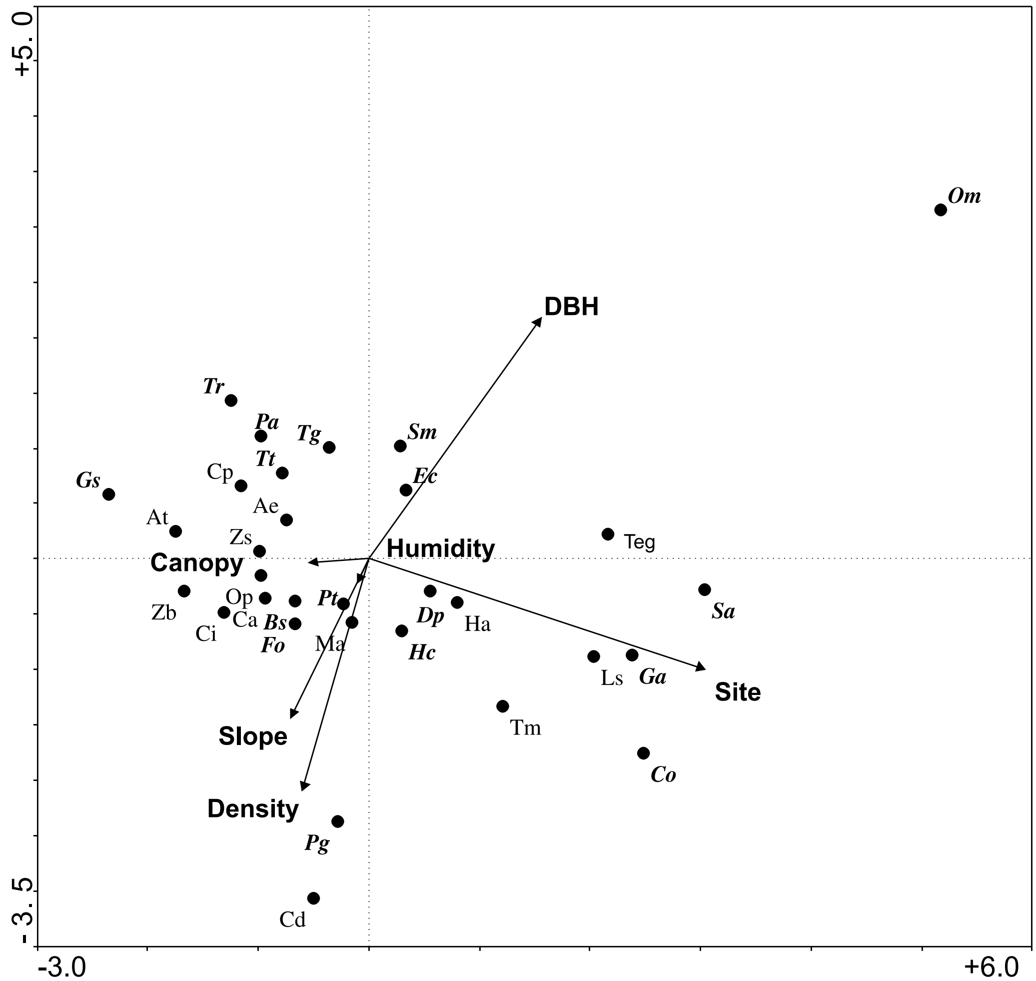
For 3 of the 10 species sampled in both natural forests and plantations, ANOVA revealed a significant difference in %C between these two habitats (Fig. 3). *Dipteryx panamensis*, *Hura crepitans*, and *Miconia argentea* showed higher C concentration in natural forests than in plantations ($F = 6.10$, $p = 0.06$; $F = 5.53$, $p = 0.06$; and $F = 8.92$, $p = 0.02$, respectively). Across the nine species studied for wood SG, C concentration and wood SG were positively correlated and linearly related ($r^2 = 0.86$, $p < 0.0003$) (Fig. 4).

## Discussion

### Importance of interspecific variations in C concentration

Our study focuses on inter- and intra-specific variation in trunk C concentration. Another study from our laboratory provided an in-depth analysis of biomass and C partitioning at the individual tree level. The data indicated that in *Tectona grandis*, tree trunk accounts for, on average, 65% of total biomass and harbors the highest C concentration of the whole tree (Kraenzel et al. 2003). In teak, soft, short-lived tissues such as small leaves and fine roots had the lowest C concentrations (46.2% and 45.2%, respectively), while the lowest third of the trunk had the highest C concentration (50.4%). Overall, woody tissues made up 95% of teak biomass, and variation in trunk C concentration with height was low (less than 0.9%). Therefore, while C concentration undeniably varies with tissue type and tree height, sampling

**Fig. 2.** Canonical correspondence analysis biplot for trunk C concentration of the 32 tree species as a function of diameter at breast height (DBH), soil humidity, canopy closure, tree density, and slope steepness. For clarity, species codes were reduced to the first and third letters (see Table 2), with the exception of *Tectona grandis*, represented by Teg, to differentiate it from *Tabebuia guyacan*. Nonpioneer codes are in bold–italic.




the trunk at breast height for C provides a good indicator of whole trunk C concentration.

Of all possible sources of variation, species was the most important in explaining variation in C concentration. Species-specific differences (38.7%) explained 10 times more variance than sites (3.4%), while ecological groups did not account for any significant variation in C concentration. That the 32 species sampled harbored significantly different C concentrations is consistent with other studies documenting interspecific variations in C sinks in tree shoots (reviewed in Kozlowski 1992). The range of trunk C concentration documented across species in this study falls within the 45–60% range for C concentration reported in different species and tissues (Kinerson et al. 1977; Houghton et al. 1985; Kauppi et al. 1995). Among all our species, the variation in C concentration was around 5%. In particular, *Tectona grandis* was singled out for having a C concentration 3.4% greater than the average for all other species combined (46.1%).

Nascimento and Laurance (2002) showed that in central Amazonian rain forests, the most important component of aboveground biomass was large (>10 cm DBH) trees. They estimated the average biomass of large trees in 1 ha of forest to be 325.5 Mg. We used our lowest (44.4%) or highest (49.5%) C concentration to estimate C stores for Nascimento and Laurance's aboveground biomass value. Use of the two C concentration values resulted in a 10% difference: 144.5 vs. 160.8 Mg C·ha$^{-1}$. The same magnitude of difference in C estimates is calculated (10%) whether we use our multi-species C concentration (46.1%) or the standard conversion factor of 50%. These simple calculations suggest that a better knowledge of species-specific C concentration could reduce the error associated with estimates of C sequestration. This might be especially useful for plantations where the low number of species would enable the proper measurement of individual species' C concentration.

## Other sources of variation in C concentration

Wood SG is considered the best indicator of wood strength and associated mechanical properties (Panshin and DeZeeuw 1980). Although most tree species have a characteristic SG, the latter generally varies with tree height (Thomas 1996), within and between individuals of the same

**Fig. 3.** Trunk C concentration for the 10 species sampled in both plantations and natural forests. Plantation trees are shown in grey, while natural forest trees are in black. Means are equivalent to the height of the bars. Vertical lines represent the standard error of the mean. The three species whose C values exhibited a statistically significant difference between plantation and natural forest individuals are indicated by an asterisk (*). Species codes are defined in Table 2.

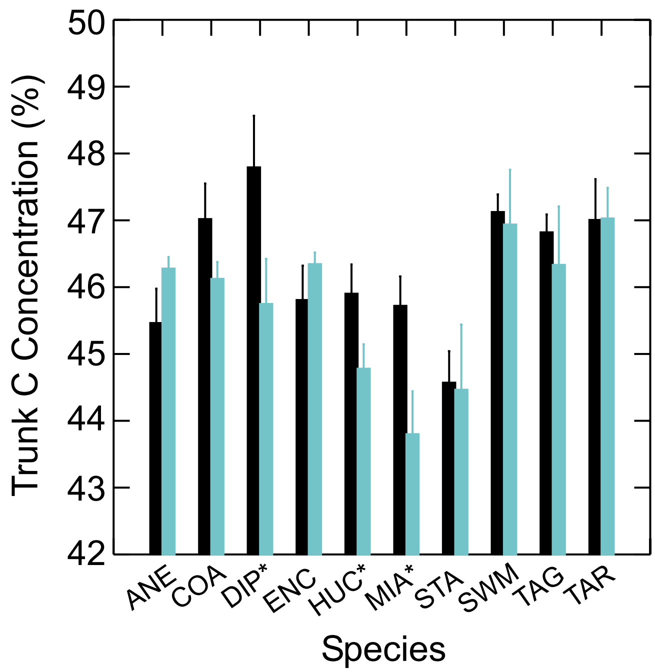
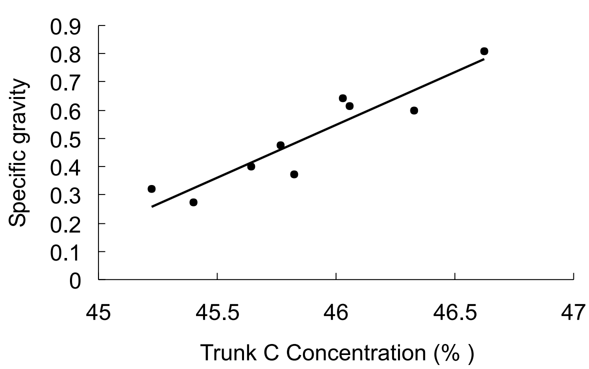



**Fig. 4.** Linear regression of wood specific gravity (SG) in function of trunk C concentration: (wood SG = 0.3732%C – 16.21, $r^2 = 0.86$, $p < 0.0003$). The nine species represented are *Anacardium excelsum*, *Cecropia insignis*, *Dipteryx panamensis*, *Faramea occidentalis*, *Luehea seemannii*, *Poulsenia armata*, *Protium tenuifolium*, *Trichilia tuberculata*, and *Zanthoxylum setulosum*.




species, as well as across species (de Castro et al. 1993). This variation reflects differences in species' chemical makeup. For instance, lipids, lignin, and protein have elevated C concentrations, while organic acids and minerals contain little and no C, respectively (Ho 1976; Poorter and Bergkotte 1992). Because wood SG is easier and cheaper to measure than trunk C concentration, we were interested in the relationship between the two traits. The strong relationship between the SG and C concentrations observed, for a subset of nine species, might pertain to the high correlation between wood density and the proportion of cell types in the wood as well as to the coupling between SG and cell wall thickness (McDonald et al. 1995).

Since metabolism and growth are manifestations of the production and storage of C-containing compounds (Kozlowski 1992), ecological grouping was examined as a potential source of variation in trunk C concentration. Shade-tolerant species have generally been associated with durable woods, tough leaves, and elevated wood density owing to their imperative need for defense (Spurr and Barnes 1980; Bazzaz et al. 1990; Condit et al. 1996). We therefore hypothesized that nonpioneer species should exhibit higher C concentrations than pioneers. Our results did not support that hypothesis (Fig. 1). Some of the highest C concentrations were obtained for *Tectona grandis* and *Ochroma pyramidale*, two undeniably fast-growing pioneers. Furthermore, several nonpioneer species exhibited some of the lowest C concentration (e.g., *Ormosia macrocalyx*, *Poulsenia armata*). Our results thus appear to refute the notion that pioneer species always have a low trunk C concentration. In a study of 37 Malaysian rain forest species, Thomas (1996) uncovered a negative relationship between wood density and maximum tree height. He suggested that canopy trees are expected to have higher growth rates, and hence, a lower wood density. In our study, some of the pioneers became tall trees, e.g., *Sterculia apetala*, while others, e.g., *Ochroma pyramidale*, never grew tall. These interspecific differences in maximum height within an ecological group might explain why the group effect was not statistically significant.

Our CCA shows that trunk C concentration across species varies with environmental and (or) growth factors (i.e., mostly sites and DBH). We believe that these two factors interact. There is an acknowledged relationship between tree age and the amount and composition of carbohydrates (Kozlowski 1992), as well as between tree age and DBH (de Castro et al. 1993). We sampled 10 species in both forests and plantations. Across these species, average DBH was approximately four times larger in natural forests than in plantations. Because the two plantations were established in 1990–1993, this difference in DBH must be linked to the relatively young age of the plantations. On the other hand, the species responding most strongly to DBH, as shown in the CCA biplot, were also the species represented by the largest individual trees. *Ormosia macrocalyx* was only sampled on roadsides in the Canal area, and its DBH ranged between 124 and 97 cm. *Enterelobium cyclocarpum* had a mean DBH of 92.1 cm in a forest environment compared with a mean DBH of 5.9 cm in plantations. This suggests that tree size and other site qualities affect trunk C concentration. However, the bulk of the observed variance in trunk C concentration can unequivocally be attributed to species.

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## References

Bassow, S.L., and Bazzaz, F.A. 1997. Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. Oecologia, **109**: 507–515.

Bazzaz, F.A., Coleman, J.S., and Morse, S.R. 1990. Growth responses of seven major co-occurring tree species of the northeastern United States to elevated $CO_2$. Can. J. For. Res. **20**: 1479–1484.

Brown, S. 1993. Tropical forest and the global carbon cycle: the need for sustainable land use patterns. Agric. Ecosyst. Environ. **46**: 31–44.

Brown, S., and Lugo, A.B. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica, **14**: 161–187.

Canadell, J.G., and Pataki, D. 2002. New advances in carbon cycle research. Trends Ecol. Evol. **17**(4): 156–158.

Chave, J., Riera, B., and Dubois, M.-A. 2001. Estimation of biomass in a neotropical forest of French Guina: spatial and temporal variability. J. Trop. Ecol. **17**: 79–96.

Condit, R., Hubbell, S.P., and Foster, R.B. 1996. Assessing the response of plant functional type to climatic change in tropical forests. J. Veg. Sci. **7**: 405–416.

Croat, T.B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif.

de Castro, F., Williamson, G.B., and de Jesus, R.M. 1993. Radial variation in the wood specific gravity of *Joannesia princeps*: the roles of age and diameter. Biotropica, **25**(2): 176–182.

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., and Bello Quintero, N. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. J. Trop. Ecol. **13**: 697–708.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisnewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science (Washington, D.C.), **263**: 185–190.

Ellis, A., Hubbell, S., and Potvin, C. 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Can. J. Bot. **78**: 1336–1347.

Ho, L.C. 1976. Variation in the carbon/dry matter ratio in plant material. Ann. Bot. (London), **40**: 163–165.

Houghton, R.A., Schlesinger, W.H., Brown, S., and Richards, J.F. 1985. Carbon dioxide exchange between the atmosphere and terrestrial ecosystems. *In* Atmospheric carbon dioxide and the global carbon cycle. *Edited by* J.R. Trabalka. US Department of Energy, Washington, D.C. DOE/ER-0239. pp. 114–140.

Houghton, R.A., Unruh, J., and Lefebvre, P.A. 1991. Current land use in the tropics and its potential for sequestring carbon. *In* Technical Workshop to Explore Options for Global Forestry Management, Bangkok, April 1991. *Edited by* D. Howlett and C. Sargent. International Institute Environment and Development, London. pp. 211–212.

Kauppi, P.E., Tomppo, E., and Ferm, A. 1995. C and N storage in living trees within Finland since 1950s. Plant Soil, **168–169**: 633–638.

Ketterings, Q.M., Coe, R., van Noordwijk, M., Ambagau, Y., and Palm, C.A. 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. For. Ecol. Manage. **146**: 199–209.

Kinerson, R.S., Ralston, C.W., and Wells, C.G. 1977. Carbon cycling in a loblolly pine plantation. Oecologia, **29**:1–10.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. Bot. Rev. **58**: 107–222.

Kraenzel, M.B., Moore, T., Castillo, A., and Potvin, C. 2003. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. For. Ecol. Manage. **173**: 213–225.

Lugo, A.E. 1992. The search for carbon sinks in the tropics. Water Air Soil Pollut. **64**: 3–9.

Lugo, A.E., Wang, D., and Bormann, F.H. 1990. Comparative analysis of biomass production in five tropical tree species. For. Ecol. Manage. **31**: 153–166.

McDonald, S.S., Williamson, B., and Wiemann, M.C. 1995. Wood specific gravity and anatomy in *Heliocarpus appendiculatus* (Tiliaceae). Am. J. Bot. **82**: 855–861.

Nascimento, H.E.M., and Laurance, W.F. 2002. Total aboveground biomass in Central Amazonian rainforests: a landscape-scale study. For. Ecol. Manage. **168**: 311–321.

Panshin, A.J., and DeZeeuw, C. 1980. Textbook of wood technology. 4th ed. McGraw-Hill Publishing Company, New York.

Poorter, H., and Bergkotte, M. 1992. Chemical composition of 24 wild species differing in relative growth rate. Plant Cell Environ. **15**: 221–229.

Schroeder, P. 1992. Carbon storage potential of short rotation tropical tree plantations. For. Ecol. Manage. **50**: 31–41.

Sedjo, R.A., and Solomon, A.M. 1989. Climate and forests. *In* Greenhouse warming: abatement and adaptation. *Edited by* N. J. Rosenberg, W.E. Easterling, P.R. Crosson, and J. Dormstadter. Resources for the Future, Washington, D.C. pp. 105–119.

Spurr, S., and Barnes, B. 1980. Forest ecology. 3rd ed. John Wiley & Sons Inc., New York.

ter Braak, C.J.F., and Smilauer, P. 1998. CANOCO 4. Centre for Biometry, Wageningen, Netherlands.

Thomas, S.C. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rainforest trees. Am. J. Bot. **83**(5): 556–566.

Vitousek, P. 1991. Can planted forest counteract increasing atmospheric carbon dioxide? J. Environ. Qual. **20**: 348–354.

Winer, B.J., Brown, D.R., and Michels, K.M. 1991. Statistical principles in experimental design. 3rd ed. McGraw-Hill Inc., New York, Toronto.

Winjum, J.K., and Schroeder, P.E. 1997. Forest plantations of the world: their extent, ecological attributes and carbon storage. Agric. For. Meteorol. **84**: 153–167.

Winjum, J.K., Dixon, R., and Schroeder, P.E. 1992. Estimating the global potential of forest and agroforest management practices to sequester carbon. Water Air Soil Pollut. **64**: 213–227.