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Abstract

In the moist tropical forest biome, which cycles carbon (C) rapidly and stores huge amounts of C, the impacts of individual species on C balances are not well known. In one of the earliest replicated experimental sites for investigating growth of native tropical trees, we examined traits of tree species in relation to their effects on forest C balances, mechanisms of influence, and consequences for C sequestration. The monodominant stands, established in abandoned pasture in 1988 at La Selva Biological Station, Costa Rica, contained five species in a complete randomized block design. Native species were: *Hieronyma alchorneoides*, *Pentaclethra macroloba*, *Viola koschnyi*, and *Vochysia guatemalensis*. The exotic species was *Pinus patula*. By 16 years, the lack of differences among species in some attributes suggested strong abiotic control in this environment, where conditions are very favorable for growth. These attributes included aboveground net primary productivity (ANPP), averaging 11.7 Mg C·ha⁻¹·yr⁻¹ across species, and soil organic C (0–100 cm, 167 Mg C/ha). Other traits differed significantly, however, indicating some degree of biological control. In *Vochysia* plots, both aboveground biomass of 99 Mg C/ha, and belowground biomass of 20 Mg C/ha were 1.8 times that of *Viola* ($P = 0.02$ and 0.03 , respectively). Differences among species in overstory biomass were not compensated by understory vegetation. Belowground NPP of 4.6 Mg C·ha⁻¹·yr⁻¹ in *Hieronyma* was 2.4 times that of *Pinus* ($P < 0.01$). Partitioning of NPP to belowground components in *Hieronyma* was more than double that of *Pinus* ($P = 0.03$). The canopy turnover rate in *Hieronyma* was 42% faster than that of *Viola* ($P < 0.01$). Carbon sequestration, highest in *Vochysia* (7.4 Mg C·ha⁻¹·yr⁻¹, $P = 0.02$), averaged 5.2 Mg C·ha⁻¹·yr⁻¹, close to the annual per capita fossil fuel use in the United States of 5.3 Mg C. Our results indicated that differences in species effects on forest C balances were related primarily to differences in growth rates, partitioning of C among biomass components, tissue turnover rates, and tissue chemistry. Inclusion of those biological attributes may be critical for robust modeling of C cycling across the moist tropical forest biome.

Keywords

abandoned pasture, biomass, carbon sequestration, carbon use efficiency, moist tropical forest, net primary productivity, plantations, root : shoot ratios, tree species effects, turnover

Disciplines

Ecology and Evolutionary Biology | Forest Biology | Natural Resources Management and Policy

Comments

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Impacts of individual tree species on carbon dynamics in a moist tropical forest environment

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Abstract. In the moist tropical forest biome, which cycles carbon (C) rapidly and stores huge amounts of C, the impacts of individual species on C balances are not well known. In one of the earliest replicated experimental sites for investigating growth of native tropical trees, we examined traits of tree species in relation to their effects on forest C balances, mechanisms of influence, and consequences for C sequestration. The monodominant stands, established in abandoned pasture in 1988 at La Selva Biological Station, Costa Rica, contained five species in a complete randomized block design. Native species were: *Hieronyma alchorneoides*, *Pentaclethra maculosa*, *Viola koschnyi*, and *Vochysia guatemalensis*. The exotic species was *Pinus patula*. By 16 years, the lack of differences among species in some attributes suggested strong abiotic control in this environment, where conditions are very favorable for growth. These attributes included aboveground net primary productivity (ANPP), averaging 11.7 Mg C·ha⁻¹·yr⁻¹ across species, and soil organic C (0–100 cm, 167 Mg C/ha). Other traits differed significantly, however, indicating some degree of biological control. In *Vochysia* plots, both aboveground biomass of 99 Mg C/ha, and belowground biomass of 20 Mg C/ha were 1.8 times that of *Viola* ($P = 0.02$ and 0.03 , respectively). Differences among species in overstory biomass were not compensated by understory vegetation. Belowground NPP of 4.6 Mg C·ha⁻¹·yr⁻¹ in *Hieronyma* was 2.4 times that of *Pinus* ($P < 0.01$). Partitioning of NPP to belowground components in *Hieronyma* was more than double that of *Pinus* ($P = 0.03$). The canopy turnover rate in *Hieronyma* was 42% faster than that of *Viola* ($P < 0.01$). Carbon sequestration, highest in *Vochysia* (7.4 Mg C·ha⁻¹·yr⁻¹, $P = 0.02$), averaged 5.2 Mg C·ha⁻¹·yr⁻¹, close to the annual per capita fossil fuel use in the United States of 5.3 Mg C. Our results indicated that differences in species effects on forest C balances were related primarily to differences in growth rates, partitioning of C among biomass components, tissue turnover rates, and tissue chemistry. Inclusion of those biological attributes may be critical for robust modeling of C cycling across the moist tropical forest biome.

Key words: abandoned pasture; biomass; carbon sequestration; carbon use efficiency; moist tropical forest; net primary productivity; plantations; root : shoot ratios; tree species effects; turnover.

INTRODUCTION

Forests generally, and moist tropical forests specifically, have huge amounts of carbon in their biomass and soils, and high rates of productivity (Dixon et al. 1994, Field et al. 1998). Forest growth, disturbance, and land use can thus have large impacts on atmospheric CO₂ levels. For example, widespread net accumulation of carbon (C) within previously cut Northern Hemisphere forests may account for one-third of the CO₂-C released by fossil fuel combustion since 1900 (Schimel et al. 2001). Indeed, it is difficult to conceive of any land-management or land-use changes that could substan-

tially mitigate continued increases in atmospheric CO₂ levels, which do not involve forests. Tropical forests, in particular, could play an important role.

In the moist tropical biome, a focus on the effects of individual tree species on forest C balances is timely because forest plantations, most of which were planted as monocultures, covered 31.3×10^6 ha of land formerly dominated by mixed-species forest by the end of 2005. Furthermore, plantation coverage has been expanding at an average of 1.8×10^6 ha/yr (Singh 1993). A better understanding of the extent to which individual tree species affect ecosystem-level C dynamics, and the mechanisms by which they do so, will enhance our understanding of human impacts on the biosphere, improve biogeochemical models, and help guide selec-

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tion of species for restoration and carbon management purposes, especially in reforestation efforts.

Our conceptual framework for exploring the effects of tree species on forest C balances (Fig. 1) is based on a modeling perspective in which species may differ in: (1) total net primary productivity (NPP); (2) partitioning of production between above- and belowground components; and (3) rates of tissue turnover. Together these traits influence the amounts, locations, and components (e.g., leaves, wood, and roots) of tree biomass present, and the growth of understory species. Together with the chemical composition of the plant components, these traits also influence (4) the quantity and quality of detritus that is produced above and below ground, which in turn influence inputs into the soil organic carbon (SOC) pool, as well as (5) outputs via soil respiration, which also includes CO₂ derived from live roots. Thus, traits of individual tree species may shift the trajectory of ecosystem development toward functionally and structurally distinct forests that differentially affect the surrounding biotic, atmospheric, and hydrologic systems within which they exist.

Our main objective was to evaluate the extent to which various C-cycling traits differed among tree species, the mechanisms by which species influenced the forest C balance, and the consequences for forest development and C sequestration. We evaluated the precepts of our conceptual framework in model systems in a tropical setting in which initial conditions were as similar as possible for all species. The experiment contained replicated plantations that had been established in abandoned pasture that had been deforested and pastured for 30 years. Although the species in this experiment were originally planted as monocultures, all plots had diverse understories at the time of this study, 15–17 years into the experiment.

Given the presence of a well-developed understory, a second objective was to determine whether differences among overstory tree species were compensated for by growth in the understory, such that C-cycling attributes at the forest level (overstory plus understory) were invariable among species. The underlying concept is that in this biome, where conditions are optimal for plant growth and species richness is high, any resources not captured by the single overstory tree species would be used by other species regenerating in the understory. The logical extension is that, even if C-cycling attributes differ among the overstory tree species, the forest-level C balance might not. This would indicate that abiotic state factors such as climate, soil, and previous land use, which are similar across species in our experiment, strongly regulate C cycling in this tropical-biome site. Alternatively, if the forest level C balance does differ among species, the effects of individual species, including their capacity to inhibit or facilitate growth of the understory, could influence the trajectory of C cycling. In that case, biotic factors, as well as abiotic factors, regulate C cycling.

We tested the following null hypotheses. For above-ground variables, we evaluated the hypotheses with respect to the overstory trees only, and also at the plot level.

1) Biomass does not differ among species. Inherent differences in growth rates among species at a common site are expected to generate differences in biomass. However, these differences may be offset by differences in mortality, maximum tree size, understory growth, or other factors that result in similar standing crops among species. To investigate why biomass might differ among species, we evaluated the following hypotheses.

2) NPP does not differ among species. The rationale is that, at the whole-forest level, abiotic factors determine plant growth in this biome, overriding inherent differences among species. We fully expect that differences among tree species exist. Our expectation is that differences in overstory tree production are compensated for by differences in understory growth.

3) Partitioning of NPP between above- and below-ground components does not differ among species. Partitioning, as used herein, refers to the proportion of total NPP that is used to construct a particular biomass component, such as bolewood (cf. Litton et al. 2007). Differences in partitioning of NPP would influence biomass accumulation because different plant components (e.g., woody and non-woody) differ in their turnover rates. Differences in partitioning would also influence the relative quantities, location, and decomposability of detrital inputs, and thus influence the quantity and turnover of soil organic carbon (SOC).

4) Rates of tissue turnover do not differ among species. A priori, we expected to reject this hypothesis because the species differ in tissue chemistry (Raich et al. 2007, Russell et al. 2007), which would be expected to drive differences in tissue longevity (e.g., Amthor 2003).

5) Rates of C sequestration do not differ among species. Rejection of this hypothesis would provide useful insight into management of reforestation efforts for mitigation of CO₂ emissions. The preceding tests are designed to provide insight into tree-based mechanisms that influence the quantity of organic C produced and stored in biomass and soil.

MATERIALS AND METHODS

Study site

This study was conducted at the La Selva Biological Station, situated in the Atlantic lowlands of Costa Rica (10°26' N, 83°59' W). Mean annual rainfall is 3960 mm and mean annual temperature is 25.8°C (Sanford et al. 1994). The native vegetation is lowland evergreen broad-leaved rain forest with abundant palms. The 12-ha experimental site is situated on a residual soil that is derived from andesitic lava flows (Alvarado 1990). The study site soil was mapped as the Matabuey consociation, Typic Tropohumult (Sollins et al. 1994), but reclassified later as Mixed Haplic Haploperox (Kleber et al. 2007). This soil is acidic, highly leached, low in

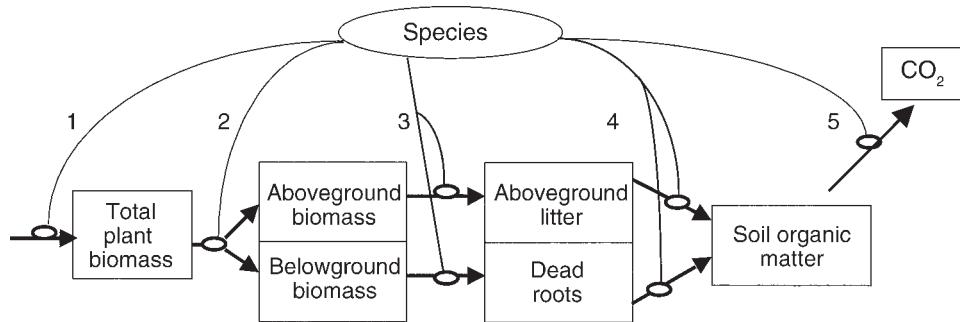


FIG. 1. Conceptual model of regulation of site carbon dynamics by plant species. Species traits have the potential to influence the following processes (curves connected to circles): (1) NPP; (2) partitioning; (3) detrital fluxes; (4) decomposition; and (5) soil respiration that includes CO_2 derived from living and dead roots, aboveground litter, and soil organic matter.

base saturation, and relatively high in organic matter. Topography of the study plots is hilly, with elevations ranging from 44 to 89 m above sea level.

Mature forest at the experimental site was cleared in 1955, the slash was burned, and pasture of *Panicum maximum* L. and *Melinis minutiflora* Pal. was established in 1956, with grazing continuous until abandonment in 1987, a typical land-use pattern in this region. This experiment was established in 1988. The randomized complete block design consisted of four blocks of twelve 0.25-ha (50 × 50 m) plots, containing 11 tree species plus an abandoned-pasture control (Fisher 1995). For the purpose of subsampling within plots, all plots were divided into four quadrats. Baseline soil data were collected in 1987, before planting (Fisher 1995).

The species used in the experiment were not selected at random; species were chosen based on farmer preferences, good growth (González and Fisher 1994), economic value, and seedling availability (Stanley and Montagnini 1999), and because they varied widely in many traits (González and Fisher 1994, Fisher 1995, Hagggar et al. 1997). The four exotic species in the original experiment were: *Acacia mangium* Willd.; *Gmelina arborea* L.; *Inga edulis* Mart.; and *Pinus patula* subsp. *tecumani* (Eguiluz & J. P. Perry) Styles, hereafter referred to as *Pinus patula*. The native species were: *Abarema adenophora* (Duke) Barneby & J. W. Grimes; *Hieronyma alchorneoides* Allemao; *Pentaclethra macroleoba* (Willd.) Kunth.; *Stryphnodendron microstachyum* Poepp.; *Virola koschnyi* Warb.; *Vochysia ferruginea* Mart.; and *Vochysia guatemalensis* Donn. Sm. Trees were planted at a spacing of 3 × 3 m. Understory vegetation in all plots was manually cleared over the first three years. The fastest-growing trees, *H. alchorneoides*, *V. ferruginea*, and *V. guatemalensis*, were thinned at age four years to about 50% of their original density (Hagggar et al. 1997). The five species that had survived until 2006, and are the subject of this study, are: *Hieronyma alchorneoides*; *Pentaclethra macroleoba* (the only N-fixing species and the dominant species at La Selva); *Pinus patula* (the only conifer); *Virola koschnyi*; and *Vochysia guatemalensis*.

The plantations were virtually abandoned in 1994 until sampling for the current study commenced in 2003. The abandoned-pasture control plots of the original experimental design were overtopped and shaded out by surrounding plots within the first three years and hence did not function as an experimental control. To provide an abandoned-pasture reference, in January 2004 we established four 14 × 8 m plots within the three-hectare abandoned pasture situated between Blocks 1 and 4. These plots had the same climate, soil type, and pre-experiment management as the plantations; the plots were dense swards of *Panicum maximum*, but had not been grazed since 1987. Four reference plots in the mature forest, situated <150 m from the experimental site, were used for soil property and basal area measurements only. For other comparisons of aboveground biomass in the mature forest, we used published values for the “Carbono – Ultisol flat” plots (Clark and Clark 2000), where soil and topography most closely resembled that of our plots. For litterfall, we used a mean of published values for “residual” soils (Vitousek 1984, Parker 1994, Davidson et al. 2002).

Biomass

Aboveground biomass.—Measurements of aboveground biomass per plot over the three-year study were based on annual inventories of all trees ≥10 cm dbh in each plot, annual inventories of all trees 2.5–10 cm in diameter in a single 3 × 15 m transect in each plot, and direct harvests of smaller woody and all non-woody (leaves, stems, flowers, and fruits) plant components.

Annual tree inventories included measurements of the dbh and heights of each tree. Heights of trees <8 m tall were measured with an extension pole; taller trees were measured with a clinometer. To convert these measurements to biomass, eight trees of each of the planted study species, encompassing the range of diameters present in the plots, were harvested from border rows in 2004 and were dissected in the field into four compartments: leaves, flowers, and fruits; twigs (diameters ≤1 cm); branches (diameters 1–10 cm); and large branches and boles (diameters ≥10 cm). All materials from each

tree were weighed fresh using an electronic hanging balance, and large subsamples were sealed tightly into plastic bags. The subsamples were weighed fresh and split into two subsamples for oven drying at 65°C for nutrient analyses and 105°C for dry mass determination. Leaves were passed through a leaf area meter (LI-COR Model LI-3100-C, LI-COR Biosciences, Lincoln, Nebraska, USA) prior to drying to determine leaf area per unit mass.

Linear regressions of total aboveground tree biomass (kg) from d^2h (diameter² × height, in m³) gave R^2 values of >0.94 for each of the planted tree species (Appendix A). The same regression form was used for each tree component, such that the sums of the components equaled total tree mass, but R^2 values were lower in those cases (Appendix A). This allowed for chemical composition of each sample to be multiplied by the mass to calculate total element storage in each component for each tree. These regression equations were applied to determine the dry biomass of and element storage in each tree over each of the three inventory years, and the per-tree data were summed within plots to determine plot-level biomass and C sequestration in living trees. The same approach was used for other tree species (>2.5 cm diameter) that colonized the plots, for which sample sizes varied (Appendix A).

Saplings (<2.5 cm diameter), shrubs (<1.5 m tall), vines, and non-woody vegetation were harvested from four 0.5 × 1.0 m quadrats per plot in early 2005. Prior to drying at 65°C, samples were divided into: woody parts; non-woody stems; leaves, flowers and fruits; aboveground standing dead materials; and aboveground roots. The dry samples were weighed and finely ground for elemental analysis.

Leaf area of each plot was estimated from leaf mass (g) × specific leaf area (SLA, m²/g). The former was estimated for each inventoried overstory and understory tree from tree basal area (Appendix A). Specific leaf areas were specifically determined for each of the harvested tree species; an average value was used for unmeasured species. The actual leaf area of understory non-woody plants, shrubs, and saplings was specifically measured as part of our understory biomass harvests.

To assess aboveground biomass in the abandoned pasture, all plant material was harvested from a single 1 × 0.5 m quadrat per transect (total $N = 4$). This material was weighed fresh and subsampled in the field to attain dry mass conversions as for the other plant material.

Belowground biomass.—We measured tree stumps and associated roots of the overstory species, woody roots located between trees, and fine roots. The stumps of three of the harvested trees per species were excavated and weighed for biomass determination. This harvest included all roots >1 cm in diameter within 1 m of the center of the stem to 1 m in depth. Considering all species together, there was a good relationship between stump root mass (kg) and aboveground tree mass (kg; $N = 15$, $R^2 = 0.95$, $P = 0.011$): $\ln(\text{stump root mass, kg}) =$

$0.8848 \times \ln(\text{aboveground tree mass}) - 1.2874$; $R^2 = 0.9057$.

This general relationship may be useful for estimating stump root mass for other tree species in the area for which data are lacking. However, analysis of variance indicated a significant effect of species (species, $P = 0.056$; species × d^2h , $P = 0.02$), so species-specific linear regressions (Appendix A) were applied to each overstory tree to estimate plot-level stump root mass. All roots >2 mm in diameter were collected from soil pits (described below) and weighed to determine woody root biomass in locations >1 m from trees. Fine roots (0–2 mm in diameter) were measured over two years using coring to sample the surface 30 cm of soil. We conducted a separate pilot study to assess the contribution of experimental species to the total fine-root biomass in the surface 15 cm, separating roots by species from one core taken from a randomly selected point within each plot. Fine roots from the 30–100 cm depth interval were collected from cores inserted horizontally into the walls of the soil pits (Valverde-Barrantes et al. 2007).

Net primary productivity

Aboveground NPP.—Aboveground fine litter production was measured in four 1.30 × 0.40 m traps per plot that were emptied twice monthly for calendar years 2004 and 2005. Collected materials were combined within plots and sorted into five categories: overstory leaves; other leaves; twigs (diameters ≤1 cm, including bark); and other materials. Larger branches were discarded from traps. The first year's data were presented by Raich et al. (2007).

Branchfall (>1 cm diameter) was collected from 3.0 × 3.0 m quadrats that were cleared of all woody debris and then were visited every three months for two years to retrieve all new branches that had fallen within them. We did not collect falling materials from dead or dying trees, which were accounted for in our tree inventories. The initial amounts of branch and bole litter present in these quadrats was used as our estimate of dead wood biomass in the plots. Everything was dried at 65°C and ground for nutrient analyses.

Tree growth was determined from our annual tree inventories of overstory and understory trees, which provided annual per-tree biomass estimates. Growth increments of each tree within each plot were summed to determine tree growth at the plot level over two years. Herbaceous vegetation was assumed to replace itself annually, so biomass was assumed equal to annual net production.

We did not measure organic matter leaching from the canopy, aboveground decomposition that would reduce masses of detritus collected in traps or quadrats, or herbivory. Therefore we underestimated aboveground net primary productivity (ANPP) by an undetermined amount (Clark et al. 2001). We have no evidence that these errors were large, with respect to what was measured, nor that they differed among species, and

therefore consider our estimates to be unbiased. We estimated total ANPP ($\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$): ANPP = tree growth + fine litter production + branchfall + growth of woody plants <1.5 m tall + herbaceous turnover.

Belowground NPP.—Robust estimation of belowground NPP (BNPP) is problematic. We measured belowground stumps and stump root growth and fine-root ingrowth, and estimated between-tree woody root growth. The growth of stumps and stump roots was estimated allometrically over two years, in parallel with aboveground tree growth measurements. The growth of woody roots between trees was estimated by multiplying the turnover rate of stumps and stump roots by woody root mass. We measured fine-root growth into 15 cm tall, plastic-mesh cylinders that were filled with root-free soil from the study plot and then reinserted vertically into the soil. Ingrowth was measured over one year (Valverde-Barrantes et al. 2007, 2009). Fine-root biomass did not vary significantly over two years of measurement (Valverde-Barrantes et al. 2007), so fine-root growth was assumed equal to fine-root production. We tested the reasonableness of our measurements using whole-soil carbon budgets (e.g., Giardina and Ryan 2002). Total in situ soil respiration was measured approximately monthly (30 times) over two years in 3–4 quadrats per plot with an LI-8100 automated soil CO_2 flux system and 8100-102 (10-cm diameter) chamber (LI-COR Biosciences, Lincoln, Nebraska, USA). Chambers were monitored for 120 s after closure; fluxes were calculated based on the final 100 s of measurements (Valverde-Barrantes 2007). The ΔSOC was calculated as the difference between measurements in 2003 and initial baseline values in 1987, as described below (also see Russell et al. 2007).

Partitioning, turnover.—Partitioning of NPP was calculated as the quotient of total belowground NPP and total aboveground NPP, expressed as a ratio. Turnover was calculated as the quotient of NPP and biomass within each component, expressed in units per year.

Carbon stocks and sequestration

Total C stocks within each plot were calculated as the sum of plant biomass C (above and below ground), soil surface detritus, and soil organic carbon (SOC) in the mineral soil to a 1-m depth. The long-term rate of C sequestration in the biomass was calculated as the total live biomass divided by 16 years, the duration of the experiment. The current rate of C sequestration was calculated as the mean change in total live biomass over years 15–17.

Detritus.—The mass of fine litter on the soil surface, including branches ≤ 1 cm in diameter, was measured three times from four locations per plot by removing and weighing everything inside a 0.11 m^2 frame (Raich et al. 2007). The mass of larger woody debris was measured in a single $3.0 \times 3.0 \text{ m}$ quadrat per plot, one

time. There were very few standing dead trees and those were not measured.

Soil.—In June–July 2003, soil properties were measured over two depth intervals, 0–15 cm (surface soil) and 15–30 cm, following the protocols of the baseline sampling of surface soil in 1987 (Fisher 1995, Russell et al. 2007). To summarize, soil was sampled at 20 randomly selected points within each quadrant, using a 3.2 cm diameter soil core in the 0–15-cm layer, and a 1.9 cm diameter core for the 15–30 cm depth. The change in soil organic carbon (0–15 cm) was calculated as the difference between values measured in the 2003 and 1987 soil samplings. Bulk density was determined for all depth intervals from soil pit measurements in the following study.

In a soil pit study, soil bulk density was determined in February–April 2005 for each of five depth intervals: 0–15, 15–30, 30–50, 50–75, and 75–100 cm. Soils in the 30–100 cm depth intervals were sampled for carbon and nutrients from soil pits, as described by Russell et al. (2007). Sampling consisted of one pit per block for each of the five species, for a total of 20 pits, with each pit $1.00 \times 0.75 \text{ m}$ in area, centered among live trees, at randomized locations.

Statistical analyses

Effects of the five tree species were evaluated using the appropriate randomized complete block model. The SAS system's GLM procedure was used for all analyses (Littell et al. 1991). Treatment (species) means were compared using Tukey-Kramer honestly significant difference (hsd) post-hoc tests with an experiment-wise error rate of $\alpha = 0.05$. We tested for homogeneity of variances and normality of distributions. The SAS system's MIXED procedure was used to evaluate whether adjustments for spatial correlations were warranted for the soil data (Littell et al. 1996). The conclusions did not differ when spatial correlations were included in the model, so we report only the results from the non-spatial models. For some variables, a single-sample *t* test was used to evaluate whether the mean across species was significantly greater than zero.

RESULTS

Leaf area index, biomass, and detrital mass

Leaf area.—By 16 years into the experiment, all species had attained a leaf area index (LAI) similar to the mature forest (Fig. 2A). Mean LAI at the plot level (all plant species combined) ranged from $5.2 \pm 0.4 \text{ m}^2/\text{m}^2$ (mean \pm SE) in *Hieronyma* to $6.5 \pm 1.0 \text{ m}^2/\text{m}^2$ in *Pentaclethra*, but the differences among species were not significant ($P = 0.723$). Neither the overstory nor understory components of LAI varied among tree species ($P = 0.34, 0.99$, respectively; Appendix D). The experimental trees accounted for 51% to 74% of the plot-level LAI (*Vochysia* and *Pentaclethra*, respectively); the greater dominance of LAI by *Pentaclethra* was marginally significant ($P = 0.074$).

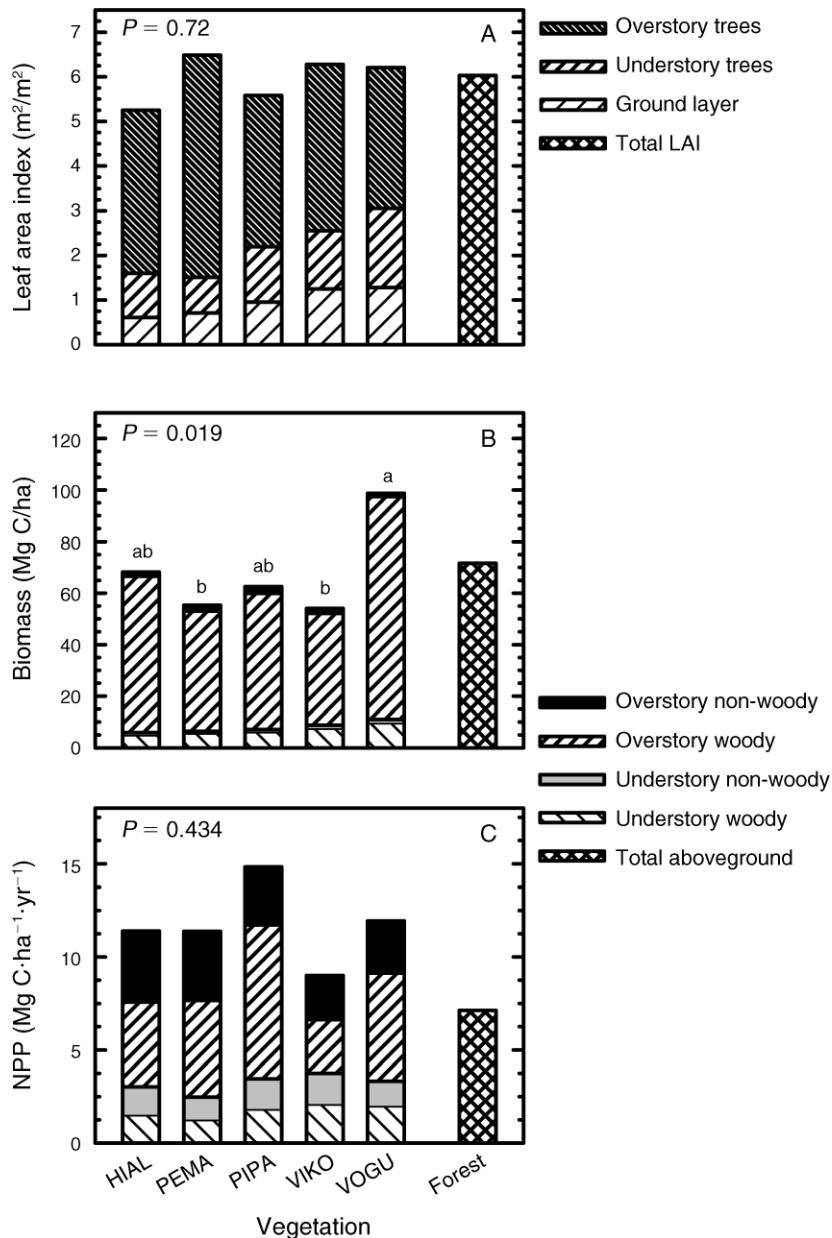


FIG. 2. Aboveground traits of five tree species in experimental plantations at La Selva Biological Station, Costa Rica. Tree species are identified by four letters, the first two letters of the species and genus (see Table 1). Values represent means over a three-year period, during years 15–17 of the experiment. Mature forest data were not included in statistical analyses. Standard errors and other statistics are provided in Appendices B, C, and D. (A) Leaf area index (LAI) by vegetation component. Mature forest data are from Clark et al. (2008). (B) Aboveground biomass by plant component. Data for the mature forest data are estimated from Clark and Clark (2000), with a 0.48 conversion factor to carbon basis for data from “Carbono – Ultisol flat” plots. Significant differences between species are denoted by different lowercase letters. (C) Aboveground net primary productivity (NPP) by plant component. Mature forest data are estimated from tree growth data (Clark et al. 2002), with the same conversion factor as in panel (B), plus the mean of values reported for fine litterfall (Vitousek 1984, Parker 1994, Davidson et al. 2002).

Aboveground biomass.—This ranged from 54 to 99 Mg C/ha in *Virola* and *Vochysia*, respectively, attaining amounts similar to the mature forest (Fig. 2B; Appendices B, D). In contrast, aboveground biomass in the abandoned pasture was 2.5 Mg C/ha. Non-woody biomass (leaves, fruits, and flowers) of the overstory

differed only marginally among the species ($P = 0.068$), ranging from 1.3 to 2.7 Mg C/ha (*Vochysia* and *Pinus*, respectively). Non-woody biomass of the understory, 0.6–1.3 Mg C/ha, was relatively invariable across species ($P = 0.213$). The understory canopy constituted 22–49% of the total canopy (*Pentaclethra* and *Vochysia*, respec-

tively). Overstorey wood biomass, ranging from 43 to 86 Mg C/ha, differed significantly among tree species ($P = 0.027$), whereas understorey wood, 5–10 Mg C/ha, did not ($P = 0.667$). Overstorey wood dominated aboveground biomass in all species, ranging from 80% of the biomass in *Virola* to 89% in *Hieronyma*. Thus, at the plot level, species differed in total (overstorey plus understorey) aboveground biomass ($P = 0.019$), with biomass in *Vochysia* plots significantly higher than that in *Pentaclethra* and *Virola*. Mean (\pm SE) basal areas in *Hieronyma*, *Pentaclethra*, *Pinus*, *Virola*, *Vochysia*, and the forest reference plots were 16.4 (\pm 0.9), 22.0 (\pm 4.0), 21.3 (\pm 1.4), 21.4 (\pm 3.7), 41.7 (\pm 3.7) and 30.8 (\pm 1.9), respectively.

Belowground biomass.—Fine-root biomass (0–100 cm) was lowest in *Pinus* and highest in *Vochysia* ($P = 0.005$; Fig. 3A; Appendices B, D). The pilot study indicated that the experimental trees dominated the fine-root biomass, with the exception of *Pinus*; in the surface 15 cm, the mean (\pm SE) fractions contributed by the experimental species were: *Hieronyma*, 0.62 (\pm 0.04); *Pentaclethra*, 0.78 (\pm 0.16); *Pinus*, 0.33 (\pm 0.08); *Virola*, 0.53 (\pm 0.11); and *Vochysia*, 0.84 (\pm 0.05). Medium-root (>2 mm and \leq 10 mm in diameter) biomass was similar across species ($P = 0.141$). Trends in belowground wood (large roots, stumps, and stump roots) followed those of aboveground wood in that *Virola* had the lowest and *Vochysia* the highest belowground wood mass ($P = 0.015$). Wood dominated the belowground biomass, such that total belowground biomass was lowest in *Virola* and highest in *Vochysia* (11 and 16 Mg C/ha, respectively; $P = 0.030$). Total biomass, above plus below ground, was significantly lower in *Pentaclethra* and *Virola*, 68 and 65 Mg C/ha, respectively, than in *Vochysia*, 119 Mg C/ha ($P = 0.014$). The plot-level root:shoot ratio of biomass was virtually constant across the species in our experiment ($P = 0.924$; Fig. 4A; Appendices B, D).

Detrital mass.—Surface detritus, dead wood, and dead fine roots was relatively low, ranging from 4.1 to 7.7 Mg C/ha (*Virola* and *Pinus*, respectively). The components (surface litter, coarse wood, and dead root mass) all differed among species ($P = 0.005$, 0.024, and 0.011, respectively; Fig. 5; Appendices B, D).

Net primary productivity

Aboveground NPP.—This averaged 11.7 Mg C·ha⁻¹·yr⁻¹, with no significant differences among species ($P = 0.433$; Fig. 2C; Appendices C, D). Non-woody (i.e., canopy) production of the overstorey differed marginally ($P = 0.099$), however, and was lowest in *Virola* and highest in *Hieronyma*. The understorey ANPP was relatively uniform across species, ranging from 2.5 to 3.7 Mg C·ha⁻¹·yr⁻¹. In all species except *Virola*, the experimental trees accounted for 72–78% of the total ANPP. *Virola* contributed only 58% of the total plot-level ANPP, but this difference was not significant ($P = 0.208$).

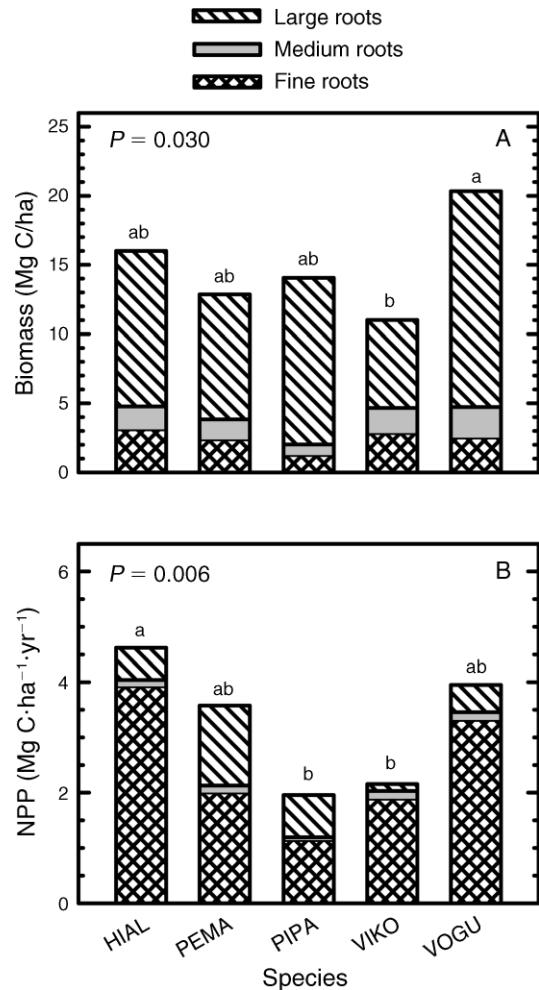


FIG. 3. Belowground traits of five tree species in experimental plantations at La Selva Biological Station, Costa Rica. Tree species are identified as in Fig. 2. Values represent means over a three-year period, during years 15–17 of the experiment. Significant differences between species are denoted by different lowercase letters. Root diameter classes are fine (\leq 2 mm), medium (>0.2–1 cm), and large (>1 cm diameter) and include stumps and stump roots, with all root categories except fine-root ingrowth measured to 1-m depth. (A) Biomass of fine, medium, and large roots. (B) Fine-root ingrowth and medium-root and large-root (belowground wood) NPP.

Belowground NPP.—In contrast to aboveground production, species differed significantly below ground, with total BNPP lowest in *Pinus*, 2.2 Mg C·ha⁻¹·yr⁻¹, and highest in *Hieronyma*, 4.6 Mg C·ha⁻¹·yr⁻¹ (Fig. 3B; Appendices C, D). These differences were driven largely by differences in fine-root production ($P = 0.002$), but large-root NPP also differed among species ($P = 0.030$).

Total NPP.—This was dominated by ANPP, which was from 1.8 to 5.9 times that of BNPP, in *Hieronyma* and *Pinus*, respectively. Thus, total NPP at the plot level did not differ significantly among species ($P = 0.404$; Appendix D) and averaged 15.0 Mg C·ha⁻¹·yr⁻¹ across species over years 15–17.

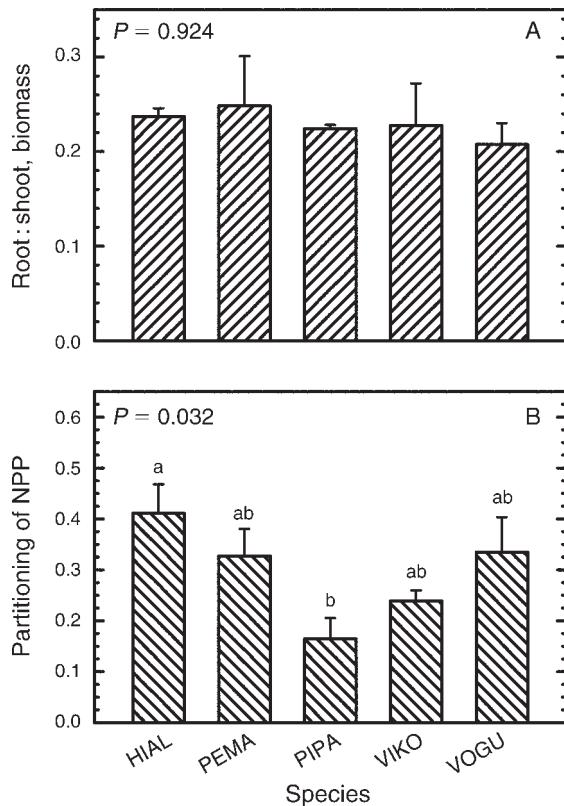


FIG. 4. Root:shoot (R:S) relationships in experimental plantations at La Selva Biological Station, Costa Rica. Tree species abbreviations are as in Fig. 2. Significant differences between species are denoted by different lowercase letters. Both biomass and NPP ratios represent total belowground carbon divided by total aboveground carbon, calculated at the plot level. Error bars represent 1 SE. (A) R:S ratio of biomass; (B) partitioning of net primary production (NPP).

Partitioning between below- and aboveground components differed significantly among species ($P = 0.032$; Fig. 4B; Appendix D). This trend was driven largely by *Hieronyma*, which partitioned heavily to belowground production in comparison with *Pinus*.

Soil

Carbon stocks.—In the surface layer (0–15 cm), carbon stocks ranged from 43.3 to 49.3 Mg C/ha, in *Pinus* and *Vochysia*, respectively, but these differences were only marginally significant ($P = 0.070$; Appendices B, D; Russell et al. 2007). Stocks of SOC (0–100 cm) ranged from 151 to 186 Mg C/ha, in *Pentaclethra* and *Vochysia*, respectively ($P = 0.113$; Appendices B, D; Russell et al. 2007).

Carbon budget.—Root and rhizosphere respiration (R_{rh}) returned an estimated 6.5 to 11.4 Mg C·ha⁻¹·yr⁻¹ to the atmosphere. The spatial variability in soil respiration was high, such that differences among species were not significant. Nevertheless, the soil respiration data provide an independent measure of belowground C dynamics, and are consistent with our

measured rates of fine-root growth, as determined from the ingrowth cores.

DISCUSSION

In an experimental setting in which land-use history and climatic and edaphic conditions were similar for all species, we evaluated three main aspects of tree species effects on forest carbon dynamics: (1) the extent to which individual species differ in their impacts on ecosystem properties and processes; (2) the plant traits that could explain these differences; and (3) the consequences for forest development and C sequestration.

Impacts of tree species

Sixteen years into this experiment, the impact of tree species on the forest C balance was substantial for some factors, but not others (Fig. 5). To place this variability in effects into perspective, it is important to recognize that the measurements of fluxes reported here represent a three-year snapshot at a middle stage of forest development. In contrast, the data for stocks represent the cumulative effects of 16 years of inputs and outputs.

Stocks.—Both of the major live stocks, aboveground and belowground biomass, were significantly influenced by the species planted, with the biomass of *Vochysia* nearly double that of *Virola* and *Pentaclethra* (Figs. 2, 5; Appendices B, D). The forest floor also differed among species in two major ways. Stocks were largest in *Pinus*, owing to a preponderance of coarse woody debris (Fig. 5; Appendices B, D). In *Hieronyma*, however, fine surface-litter mass was more than double that of *Virola* (Appendices B, D). These data suggest that the different species create markedly different habitats for forest-floor fauna.

The extent to which biomass root:shoot (R:S) ratio varies among species has important implications for evaluation of C sequestration because aboveground biomass is a widely used metric (e.g., Houghton and Goetz 2008), whereas belowground biomass is infrequently measured. This can be a source of uncertainty, as R:S ratio of biomass can vary among tree species (Cuevas et al. 1991). In our site, the large root (stump + stump roots)-to-shoot allometries of the species were significantly different (Appendix A). The biomass of small roots also differed, however, with trends among species the opposite of those for large roots. Thus, differences among species in large-root biomass were counter-balanced by differences in small roots, such that the total plot-level R:S ratio was invariable, averaging 0.23 (± 0.01 SE) across species (Fig. 4A; Appendices B, D).

The mineral soil to 1-m depth accounted for 66% of the C in the system, but species effects were not significant (Fig. 5; Appendices B, D). Organic C below the surface soil is not particularly vulnerable to the rapid, wholesale losses from fire and harvest that can eliminate aboveground biomass C stocks, and acted as a large, relatively stable C storage component at our sites.

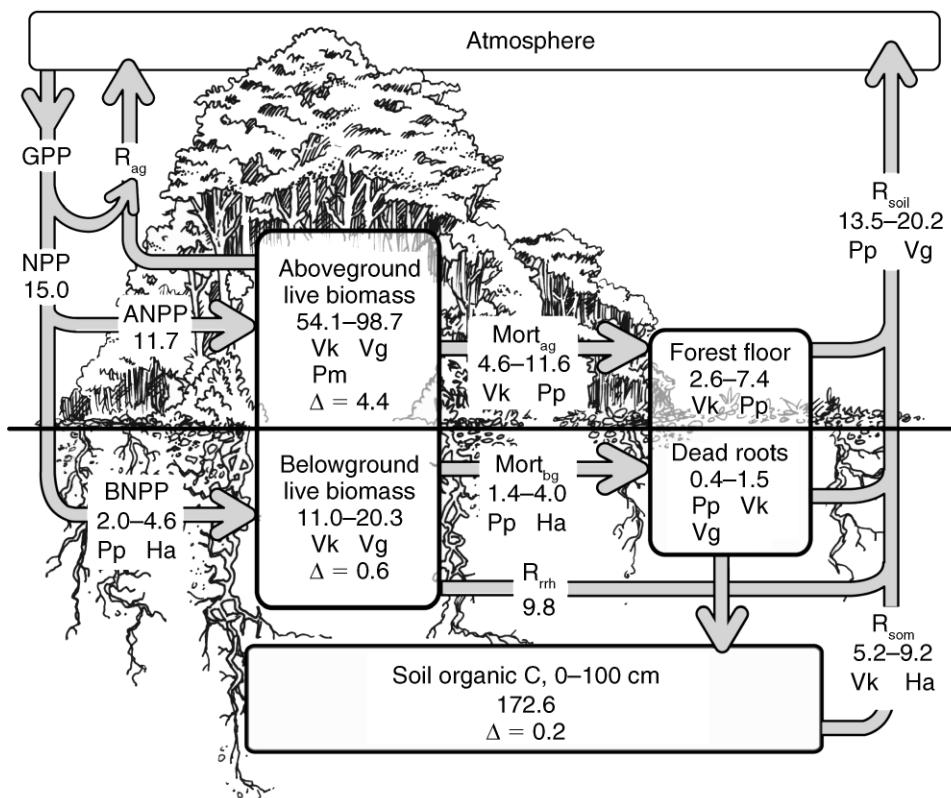


FIG. 5. Species effects on forest carbon balances in the experimental site at La Selva Biological Station. Fluxes ($Mg\ C\ ha^{-1}\ yr^{-1}$) and stocks ($Mg\ C/ha$) differ significantly where species acronyms are listed below the minimum and maximum for the variable. Otherwise, the mean across species is shown. Species abbreviations are: *Ha*, *Hieronyma alchorneoides*; *Pm*, *Pentaclethra macroloba*; *Pp*, *Pinus patula*; *Vk*, *Virola koschnyi*; *Vg*, *Vochysia guatemalensis*. Full results of statistical tests are in Appendices B, C, and D. $Mort_{ag}$, $Mort_{bg}$, and R_{ag} represent above- and belowground mortality and aboveground respiration, respectively. Gross, aboveground-net, belowground-net, and total net primary productivity are denoted by GPP , $ANPP$, $BNPP$, and NPP , respectively. Other variables are defined in Table 1. Soil organic carbon data are adapted from Russell et al. (2007).

Fifty years after the forest was cut, burned, and converted to pasture, SOC stocks to 1-m depth were similar to those in undisturbed forest (Russell et al. 2007).

Processes.—At this stage of forest development, the most striking differences among species were in belowground processes (Fig. 5). In particular, fine-root growth was significantly higher in some species, *Hieronyma* and *Vochysia*, whereas *Pentaclethra* excelled in large-root growth (Figs. 3, 5; Appendices C, D). The soil C budgets indicated that fine-root growth may have been underestimated, in that estimated carbon use efficiencies (CUEs) for root production were quite low (Table 1) in comparison to previous estimates (see Litton et al. 2007). This is reasonable, considering that we did not measure fine-root growth below 15 cm, and that the root-ingrowth method may miss the turnover of very fine roots (Fahey and Hughes 1994).

Partitioning of NPP to belowground components was highest in *Hieronyma*, 0.41, compared with 0.19 in *Pinus*. The differences among species in belowground CUE (Table 1) were best explained by differences in

partitioning between wood and fine roots. *Hieronyma* had the highest partitioning to wood in the belowground components. Because wood has a relatively higher CUE than fine roots (Litton et al. 2007), *Hieronyma* had the highest belowground CUE.

Species differed in the turnover of various components: in particular, turnover rates of the canopy were faster in *Hieronyma* than in *Virola*, by 42% ($P = 0.002$; Appendix D; Fig. 6A). Turnover of fine-roots (Fig. 6B) and stump roots also varied ($P = 0.082$ and 0.004 , respectively), whereas aboveground woody components did not (Appendix D).

Aboveground mortality was marginally higher in *Pinus* than in *Virola* ($P = 0.066$), while belowground mortality was highest in *Hieronyma* and lowest in *Pinus* and *Virola* ($P = 0.011$; Fig. 5; Appendices C, D). Once the canopy litter reached the forest floor, decay rates in *Pentaclethra*, 2.8/yr, were nearly double those of *Vochysia*, 1.5/yr (Raich et al. 2007). Belowground, however, *Vochysia* fine roots decayed very rapidly, seven times faster than did fine roots of *Virola* (Raich et al. 2009).

TABLE 1. Soil carbon budgets in plantations of five experimental tree species in lowland Costa Rica.

Species	R_{soil}	Litterfall	ΔSOC	BNPP	Fine-root ingrowth
<i>Hieronyma alchorneoides</i>	17.40 ^{ab} ± 1.81	5.49 ^a ± 0.13	0.25 ± 0.13	4.62 ^a ± 0.77	3.93 ^a ± 0.51
<i>Pentaclethra macroleoba</i>	16.72 ^{ab} ± 1.84	5.09 ^{ab} ± 0.32	0.14 ± 0.06	3.57 ^{ab} ± 0.56	2.00 ^{bc} ± 0.24
<i>Pinus patula</i>	13.54 ^b ± 0.93	4.76 ^{ab} ± 0.31	-0.03 ± 0.07	1.96 ^b ± 0.07	1.15 ^c ± 0.14
<i>Virola koschnyi</i>	15.93 ^{ab} ± 0.74	3.56 ^c ± 0.31	0.22 ± 0.08	2.16 ^b ± 0.38	1.90 ^{bc} ± 0.26
<i>Vochysia guatemalensis</i>	20.18 ^a ± 0.88	4.26 ^{bc} ± 0.13	0.32 ± 0.05	3.95 ^{ab} ± 1.02	3.32 ^{ab} ± 0.68

Notes: All fluxes are $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, mean ± SE. Means within a column followed by the same letter do not differ significantly among species (Tukey's hsd, $P=0.05$). Fine-root ingrowth is for the surface 15 cm of soil only. Decay was estimated as: litterfall + fine-root ingrowth - ΔSOC . Root and rhizosphere respiration (R_{rrh}) was estimated from $R_{\text{soil}} - \text{Decay}$. Carbon use efficiency of roots (CUE_{BNPP}) was estimated from total BNPP/(total BNPP + R_{rrh}). R_{soil} , litterfall, and ΔSOC values represent means of years 16–17, 15–16, and 0–16, respectively. Fine-root data (from year 16) are based on Valverde-Barrantes et al. (2007, 2009).

Mechanisms of influence

Compensatory effects.—We evaluated the effect of the understory with respect to the total forest C balance. The initial site preparation in 1988 had removed the understory, effectively reducing species richness to one species at the onset of the experiment. Within the first five years, woody regeneration differed among the species (Haggar et al. 1997, Powers et al. 1997). By 16 years, the site had become home to 255 vascular plant species (sampled area = 3.8 ha; Bedoya Arrieta 2009). This understory contributed leaf area index, biomass, and NPP to the plots (Fig. 2). Thus, it appears that this species-rich understory flora was capable of capturing resources that the overstory trees did not. However, the biomass and NPP of the understory in years 15–17 were relatively invariable across overstory tree species. Thus, differences among overstory tree species in C-cycling attributes were not compensated for by the understory, and remained evident at the level of the whole forest. We conclude that the traits of individual species can exert a significant and discernible influence on the forest C balance, even in this species-rich environment where abiotic factors strongly promote plant growth.

Carbon dynamics.—*Hieronyma* and *Vochysia* have had the biggest impacts on the magnitude of C cycling in these systems, but by very different means. *Hieronyma* could be characterized as a “high throughput” species. It was highly productive, especially below ground, but partitioned relatively more to components having fast turnover rates in comparison with the other species (Fig. 5). The relatively higher partitioning to roots in *Hieronyma* did not translate into significantly higher SOC, however (Russell et al. 2007), perhaps because decay of soil organic matter (R_{som}), was also high (Table 1, Fig. 5).

In contrast to *Hieronyma*, the species with the largest C accumulation both in biomass and soil, *Vochysia* (Fig. 5), was intermediate in its partitioning to roots, and in rates of detrital production and turnover (Figs. 2C, 4B, 6). Despite the lack of significant difference among species in bolewood growth in years 15–17, the difference in wood biomass suggests that inherent differences in growth rates over the history of the experiment have generated the currently observed

differences in biomass carbon among species. During the first five years of this experiment, *Vochysia* trees were consistently larger (González and Fisher 1994), and this trend has continued into years 15–17 (Fig. 7). We infer that *Vochysia* has achieved its high rate of carbon sequestration through high rates of production throughout its lifespan to date (Fig. 7).

Tissue chemistry.—The species differed in multiple ways in the chemistry of their senesced leaves and fine roots (Raich et al. 2007, Russell et al. 2007). We

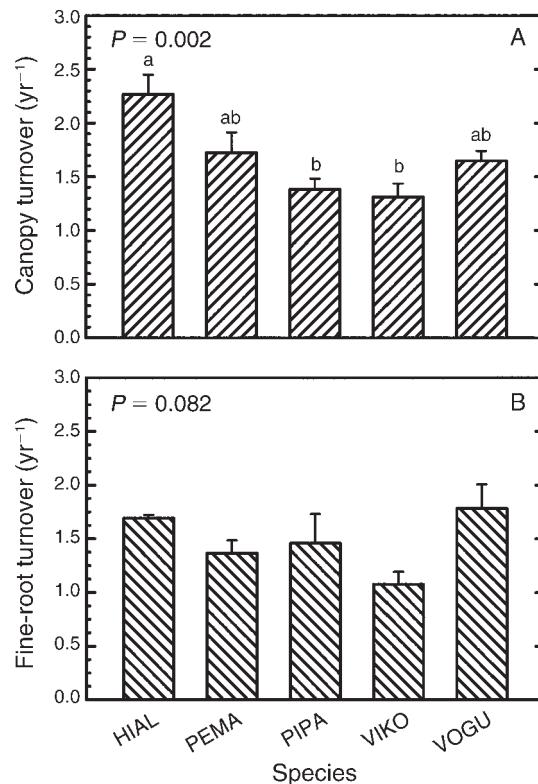


FIG. 6. Turnover of short-lived plant components. Tree species abbreviations at the La Selva site are as in Fig. 2. Significant differences between species are denoted by different lowercase letters. Error bars represent 1 SE. (A) “Canopy” turnover includes leaves, flowers, fruit, and twigs. (B) Fine-root turnover is based on Valverde-Barrantes et al. (2007, 2009).

TABLE 1. Extended.

Decay (R_{som})	R_{roots} (R_{rrh})	CUE _{BNPP}
9.17 ^a ± 0.53	8.23 ± 2.15	0.39 ^a ± 0.07
6.95 ^b ± 0.34	9.77 ± 1.51	0.28 ^{ab} ± 0.05
5.94 ^b ± 0.23	7.60 ± 0.74	0.21 ^{ab} ± 0.02
5.23 ^b ± 0.40	10.70 ± 0.69	0.17 ^b ± 0.02
7.27 ^b ± 0.82	12.91 ± 0.48	0.23 ^{ab} ± 0.03

hypothesize that these differences played an important role in driving many of the observed differences in processes. For example, *Vochysia* is an aluminum accumulator in this site (Russell et al. 2007), which may explain its relatively slower aboveground decomposition rate.

Consequences for carbon cycling

Tropical forest loss rates, as high as 152 000 km²/yr (Hassan et al. 2005), were associated with the release of 1.6 Pg C/yr in the 1990s (Denman et al. 2007), accounting for nearly 20% of anthropogenic greenhouse gas emissions in that decade (Gullison et al. 2007). Following deforestation and subsequent agricultural use, land is often abandoned, a land-use category that represents roughly half the landscape in the tropics (Silver et al. 2000). Given the magnitude of area in this land-use category, management of abandoned agricultural land has important consequences for the global C cycle.

Forest development.—Each of the five species remaining in these experimental plantations has promoted reforestation of this site, by nearly all measures. In all species, LAI, biomass, and SOC content were roughly equivalent to that of the mature forest by 16 years (Fig. 2; Russell et al. 2007). However, they remain monodominant plantations, with floristic compositions that are very different from nearby mature forest (Bedoya Arrieta 2009). Also, potential C mineralization of SOC was lower in all species in comparison with the mature forest, suggesting that some aspect of the soils had not yet recovered from the land-use changes (Russell et al. 2007). Nevertheless, these plantations have, after fewer than 20 years, become forests.

In contrast to the plantations, the abandoned pasture reference plots attained an aboveground biomass ~3% that of *Vochysia*, despite the high growth potential at this site. Without active reforestation efforts, the adjacent abandoned pasture in our site remained in arrested succession (*sensu* Lugo and Helmer 2004). Thus, the plantations have not obviously served to accelerate forest development on nearby lands, as suggested by Rey Benayas et al. (2008). Presumably, competition from the long-established grasses has prevented seed germination and/or seedling establishment, a situation that is widespread in abandoned farmland in Central America (Hooper et al. 2002).

Most species in these plantations had higher rates of production than the mature forest (Fig. 2C). Tree growth, on an organic matter (OM) basis, ranged from 5.5 to 9.9 Mg·ha⁻¹·yr⁻¹ in the plantations (*Virola* and *Vochysia*, respectively), compared with 5.5 Mg·ha⁻¹·yr⁻¹ in the mature forest (Clark et al. 2002). Fine-litter production in the plantations was 7.0–11.0 Mg·ha⁻¹·yr⁻¹ (*Virola* and *Hieronyma*, respectively), in comparison with 8.7 Mg·ha⁻¹·yr⁻¹ in the mature forest (Parker 1994). Aboveground NPP (tree growth + fine litter production) in the plantations was 12.5–19.4 Mg·ha⁻¹·yr⁻¹ (*Virola* and *Hieronyma*, respectively), compared with an estimated 14 Mg·ha⁻¹·yr⁻¹ in the mature forest. Our more complete estimates of ANPP, which include branchfall and understory ANPP, range from 18.4 to 24.7 Mg·ha⁻¹·yr⁻¹ (*Virola* and *Hieronyma*, respectively). By 16 years, aboveground biomass in *Hieronyma* and *Vochysia*, at 141 and 211 Mg/ha, respectively, equaled or surpassed that of the mature forest, 149 Mg/ha (Clark and Clark 2000). This phenomenon of higher biomass accumulation and rates of C cycling in younger forests, where presumably

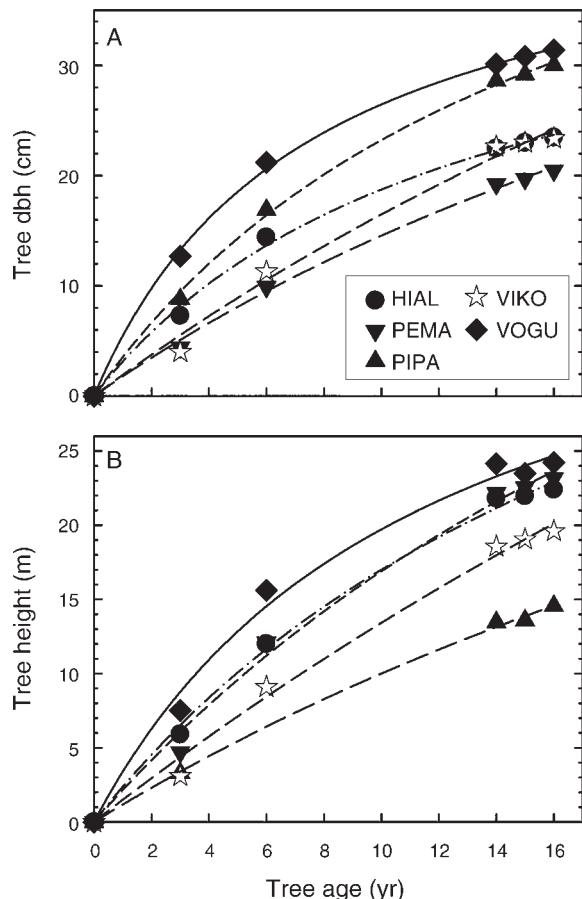


FIG. 7. Tree growth in the experimental site at La Selva Biological Station during years 0–17. Species abbreviations are as defined in Fig. 2. Data for years 0–6 are from González and Fisher (1994) and Haggard et al. (1997).

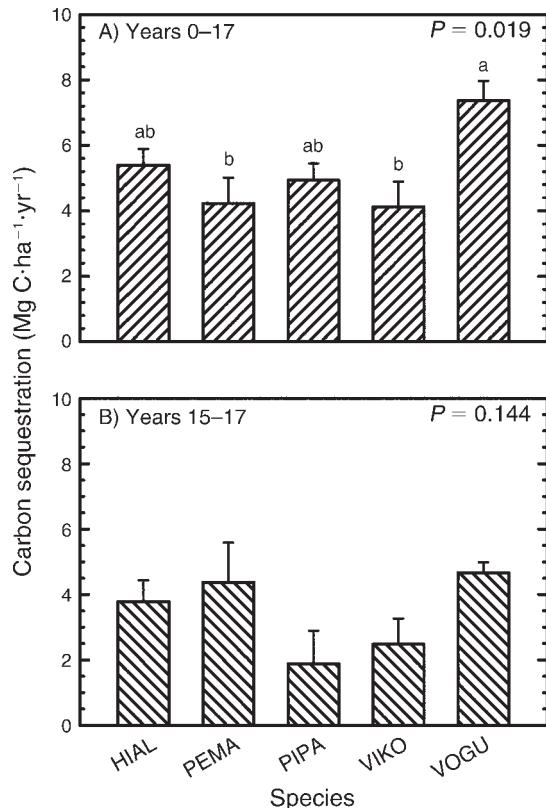


FIG. 8. Carbon sequestration in live biomass in the experimental site at La Selva Biological Station for (A) years 0–17 and (B) years 15–17. Species abbreviations are as defined in Fig. 2. Significant differences between species are denoted by different lowercase letters. Error bars represent 1 SE.

respiration and/or mortality are lower, has been documented in a variety of other systems, from plantations in the temperate zone (Malmsheimer et al. 2008) to secondary forests in the tropics (Brown and Lugo 1990).

Carbon sequestration.—Total C sequestration in biomass (aboveground plus belowground) over the 16-yr course of the experiment differed among the species ($P = 0.019$), with rates ranging from 4.1 to 7.4 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in *Virola* and *Vochysia*, respectively (Fig. 7A; Appendices B, D). Even by years 15–17 the rates continued to be high, averaging 3.44 (± 0.42) $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ across years and species, although differences among species had evened out at this more advanced stage ($P = 0.144$; Fig. 7B). Carbon sequestration rates were still significantly positive in these 16-yr-old trees ($P < 0.0001$), indicating that the plantations have not yet reached their full potential for C accumulation. We do not know what that potential might be, but our data suggest that the mature forest biomass does not represent an upper limit, or biomass asymptote.

Although SOC accumulation rates in the surface soil were similar among the species (Table 1, Fig. 5), the

mean rate across species was significantly positive ($P = 0.0005$). On average, the surface soil in the plantations had been accumulating 0.18 (± 0.04) $\text{Mg C}/\text{ha}$ in each year over the last 16 years. Baseline data were not available deeper in the profile, but SOC stocks in year 16 were similar among the plantations, abandoned pasture, and mature forest reference plots. Thus, our findings echoed those of Schedlbauer and Kavanagh (2008): in this soil type, SOC storage in deeper soil appeared relatively unchanged by land-use change.

Multiple factors vary among locations, such that comparisons across locations are confounded, but in general, biomass and rates of C accumulation at our site were intermediate between those reported for secondary forests and highly managed plantations of exotic species. In secondary succession in Puerto Rico, aboveground biomass (on an organic matter basis) increased at a rate of 6.2 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ during the first 20 years (Silver et al. 2000), compared with the range of 6.1–11.7 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ measured across species in our site. Silver et al. (2000) also reported rates of 2.9 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ during 80 years of secondary succession, highlighting the long-term potential of trees to sequester C.

In plantations of exotic species in Hawaii, aboveground biomass of *Albizia facaltaria* (L.) Fosberg and *Eucalyptus saligna* Sm. averaged 216 and 323 Mg/ha (OM basis), respectively, by 16 years (Binkley and Ryan 1998). By comparison, species in our site varied from 116 to 211 Mg/ha at this age (*Pentaclethra* and *Vochysia*, respectively). The *Albizia* and *Eucalyptus* trees were from genetically selected stocks, whereas trees in our study were from wild-type seed sources. The lower biomass in our site may be related to the unimproved seed sources, inherently lower soil fertility, and/or less intensive management; essentially, there was no management following canopy closure, which was 3–6 years across species. This less intensive management regime, and intermediate rates of C sequestration, are perhaps more typical of reforestation projects by landowners in Central America. Under similar management as in our study, aboveground biomass in 20-yr-old plantations of an exotic species, *Tectona grandis* Linn., averaged 100–141 Mg/ha across sites in Panama (Kraenzel et al. 2003). In other plantations on different soils at La Selva, aboveground biomass in 12–13-yr-old plantations was estimated to be 89, 101, and 105 Mg/ha in *Hieronyma alchorneoides*, *Virola koschnyi*, and *Vochysia guatemalensis*, respectively (Redondo-Brenes and Montagnini 2006).

The rate of C sequestration in these plantations was 5.2 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, averaged over the last 17 years and across species (Fig. 8A). This roughly equals the mean annual per capita fossil fuel use in the United States, which averaged 5.3 Mg C during the time span under consideration in this study, 1988–2005 (Marland et al. 2008). Of course, this per capita rate of CO_2 production varies through time, but it does provide a perspective on

the capacity of these plantations to mitigate CO₂ emissions. Approximately one hectare of these plantations has been sequestering the CO₂ produced by one average American over each of the last 17 years. Given the large area of abandoned agricultural land in the moist tropics, and the huge potential for tree growth, reforestation in this biome could become an important component within a multifaceted approach for mitigation of atmospheric CO₂ concentrations.

We used experimental single-species tree plantations as model systems to identify mechanisms by which individual tree species may influence C-cycling attributes at the whole-forest level, and to quantify the magnitudes of their impacts, in a single environment. We found no significant effects of species on total NPP or SOC accumulation to one-meter depth. Those results indicate relatively strong abiotic (vs. species) control over those attributes. On the other hand, among just five tree species we observed significant differences in partitioning of NPP among biomass components, tissue turnover rates, aboveground and belowground biomass and detritus, and in belowground C-cycling processes including soil respiration, heterotrophic respiration, and belowground NPP (Fig. 5). We suggest that these different results can be attributed primarily to differences among species in (1) growth rate, (2) carbon use, and (3) tissue chemistry. Inclusion of those biotic attributes may be essential for robust modeling of C cycling across the many forest types that comprise the moist tropical forest biome.

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APPENDIX A

Biomass regressions for the trees at the experimental site at La Selva Biological Station, Costa Rica (*Ecological Archives* A020-037-A1).

APPENDIX B

Carbon stocks in biomass, detritus, and soil organic matter in plantations of five experimental tree species in lowland Costa Rica (*Ecological Archives* A020-037-A2).

APPENDIX C

Net primary productivity (NPP), turnover, mortality, and carbon sequestration in plantations of five experimental tree species in lowland Costa Rica (*Ecological Archives* A020-037-A3).

APPENDIX D

Statistical results for responses measured at the experimental site at La Selva Biological Station, Costa Rica (*Ecological Archives* A020-037-A4).