

CARBON SEQUESTRATION AND PLANT COMMUNITY DYNAMICS FOLLOWING REFORESTATION OF TROPICAL PASTURE

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Abstract. Conversion of abandoned cattle pastures to secondary forests and plantations in the tropics has been proposed as a means to increase rates of carbon (C) sequestration from the atmosphere and enhance local biodiversity. We used a long-term tropical reforestation project (55–61 yr) to estimate rates of above- and belowground C sequestration and to investigate the impact of planted species on overall plant community structure. Thirteen tree species (nine native and four nonnative species) were planted as part of the reforestation effort in the mid to late 1930s. In 1992, there were 75 tree species (>9.1 cm dbh) in the forest. Overall, planted species accounted for 40% of the importance value of the forest; planted nonnative species contributed only 5% of the importance value. In the reforested ecosystem, the total soil C pool (0–60 cm depth) was larger than the aboveground C pool, and there was more soil C in the forest (102 ± 10 Mg/ha [mean \pm 1 SE]) than in an adjacent pasture of similar age (69 ± 16 Mg/ha). Forest soil C (C_3 -C) increased at a rate of ~ 0.9 Mg·ha⁻¹·yr⁻¹, but residual pasture C (C_4 -C) was lost at a rate of 0.4 Mg·ha⁻¹·yr⁻¹, yielding a net gain of 33 Mg/ha as a result of 61 years of forest regrowth. Aboveground C accumulated at a rate of 1.4 ± 0.05 Mg·ha⁻¹·yr⁻¹, to a total of 80 ± 3 Mg/ha. A survey of 426 merchantable trees in 1959 and 1992 showed that they grew faster in the second 33 years of forest development than in the first 22 years, indicating that later stages of forest development can play an important role in C sequestration. Few indices of C cycling were correlated with plant community composition or structure. Our results indicate that significant soil C can accumulate with reforestation and that there are strong legacies of pasture use and reforestation in plant community structure and rates of plant C sequestration.

Key words: biodiversity; biomass; C isotopes; C sequestration; Luquillo Experimental Forest; nonnative species; productivity; Puerto Rico; tropical reforestation.

INTRODUCTION

Over the last two decades considerable research has been directed at understanding the effects of deforestation and land use change on ecological processes in tropical ecosystems. This work has documented adverse consequences of global significance including high rates of C emissions to the atmosphere (Lugo and Brown 1980, Houghton et al. 1987, Dixon et al. 1994, Veldkamp 1994, Neill et al. 1996) and losses of biodiversity (Wilson 1988, Whitmore and Sayer 1992). As economic development proceeds in tropical countries, land use practices change, and degraded land is abandoned. Some of this land is reforested either through natural succession or through assisted succession and plantation establishment. The area of secondary forest and plantations in the tropics now exceeds the area of mature forest (Lugo and Brown 1992, FAO 1993).

Reforestation has been proposed as a means to help offset C losses through the accumulation and long-term storage of C in plant biomass and soil organic matter (Lugo 1992, Brown et al. 1996, Fearnside and Guimarães 1996). Winjum et al. (1992) estimated that 52–104 Pg of C could be sequestered over 50 years through reforestation and afforestation globally, with $\sim 70\%$ occurring in tropical latitudes. Significant amounts of C can accumulate in plants and soils within the first 20 years of forest regrowth (Brown and Lugo 1992, Silver et al. 2000a), and aboveground C pools can exceed 100 Mg/ha in humid secondary forests after just 50 years (Lugo and Brown 1992). Unlike aboveground biomass, which always increases with reforestation, soil C from the previous land use can be lost simultaneously with an increase in forest-derived C inputs. Tropical pastures often store more soil C than mature tropical forests (Detwiler 1986, Neill et al. 1996), and thus tropical reforestation can result in a decrease in soil C pools. Significant losses of residual soil C have recently been reported during early secondary succession (Rhoades et al. 2000) and from young plantations (Bashkin and

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TABLE 1. Tree species planted in the Cubuy Annex of the Luquillo Experimental Forest, Puerto Rico.

Species	Family	Status
<i>Brysonima spicata</i> (Cav.) H.B.K.	Malpighiaceae	native
<i>Calophyllum antillanum</i> Britton	Guttiferae	native
<i>Casuarina equisetifolia</i> L.	Casuarinaceae	non-native
<i>Cedrela odorata</i> L.	Meliaceae	native
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae	native
<i>Hymenaea courbaril</i> L.	Leguminosae	native
<i>Lucuma multiflora</i> (A. DC) Eyma	Sapotaceae	native
<i>Petitita domingensis</i> Jacq.	Verbenaceae	native
<i>Swietenia macrophylla</i> King	Meliaceae	non-native
<i>Swietenia mahagoni</i> Jacq.	Meliaceae	non-native
<i>Tabebuia heterophylla</i> (DC) Britton	Bignoniaceae	native
<i>Tectona grandis</i> L. f.	Verbenaceae	non-native
<i>Thespesia grandiflora</i> DC	Malvaceae	endemic

Note: Nomenclature follows Little and Wadsworth (1989) and Molina and Alemañ (1997).

Binkley 1998, Binkley and Resh 1999). The degree to which these short-term patterns persist over long time periods is unknown. The eventual, long-term effects of reforestation on soil C pools represent an important missing piece of information for evaluating reforestation as a C offset option.

The plant community composition and structure of reforested ecosystems often differs from mature forest ecosystems (Lugo 1992). Reforested ecosystems often consist of a mix of planted and naturally regenerated species. Both native and nonnative species are planted for reforestation; nonnative species are often chosen for reforestation when native species are difficult to establish (Evans 1992). The use of nonnative species in reforestation has raised concerns about the long-term effects of nonnatives on the establishment and viability of native species (Lamb 1998). Although increased biodiversity is often an added benefit of reforestation in the tropics, initial planting tends to result in lower biodiversity, higher dominance, and different species composition than natural secondary forests (Lugo 1992). The presence of planted native and nonnative species is likely to affect C dynamics. Species composition and dominance impact the amount and mean residence time of C in the ecosystem through effects on plant growth rates, C allocation patterns, and C quality (Hobbie 1992, Lugo 1992). Understanding the long-term effects of reforestation on plant community characteristics and the subsequent impact on C dynamics will provide managers and policy makers with useful tools for maximizing C sequestration and biodiversity.

In this study, we used a long-term tropical reforestation project to explore the effects of forest re-establishment on above- and belowground C pools, rates of C accumulation, plant community composition, and ecosystem structure. The well-documented land use history and the availability of earlier vegetation surveys conducted at this site enabled us to estimate the effects of past land use on soil C dynamics and the effects of planted species on the present day plant community structure, biodiversity, and above- and below-

ground C sequestration in a reforested tropical ecosystem.

METHODS

Site description

The study was conducted in the Cubuy Annex of the Luquillo Experimental Forest (LEF), Puerto Rico (18°10' N, 65°30' W), part of the National Science Foundation (NSF) sponsored Long-Term Ecological Research program. The region ranges in elevation from ~300–550 m above sea level, and is in the subtropical moist forest life zone (sensu Holdridge et al. 1971). Estimated annual rainfall is ~2500 mm based on comparisons with nearby stations in the LEF. June through November are wetter months, while January through May are drier. Soils in the Cubuy region are ultisols derived from volcanoclastic material with dioritic intrusions. Soils are generally highly weathered, well drained, and have clay and clay loam textures.

In the mid to late 1930s, the U.S. Forest Service conducted a reforestation project on 185 ha of pastureland in the Cubuy region of the Luquillo Mountains using a combination of planting and natural regeneration (Marrero 1947). Aerial photographs show that the region was devoid of over 95% of the original forest cover at the start of the reforestation effort; there is no remaining mature forest in this life zone in Puerto Rico. Nine native species and four nonnative species were planted (Table 1). In 1959, the U.S. Forest Service established 116 0.04-ha permanent circular plots at 100 × 100 m spacings distributed throughout an area (~9 ha) of contiguous forest. According to interviews with owners of adjacent land, this area was one large holding when in pasture, was never fertilized, and was moderately grazed. All merchantable trees >9.1 cm diameter at breast height (dbh, 1.37 m above the ground) were identified to species and tagged. Whether or not a tree was merchantable was based on size and form, regardless of species. In 1992, all trees >9.1 cm dbh were identified to species and measured (dbh). No-

menclature follows Molina and Alemañy (1997) and Little and Wadsworth (1989).

The 116 permanent plots and adjacent pastures offered a rare opportunity to explore changes in ecosystem C dynamics and plant community composition and structure over a long time period, longer than is typically viable for a single researcher or group. Long-term studies such as this are valuable for exploring the trends with reforestation, afforestation, and restoration activities that characteristically require long time periods to reach a degree of stability. These types of studies are not without problems, however. One constraint in the current study is lack of an existing mature forest in the region to use as a reference of old growth biomass, C pools, and diversity. Furthermore, studies such as these must often rely on narrative or recorded historical information on past land use to reconstruct patterns in ecosystem change over time (as opposed to direct observation). One strength of this study is that we combined the use of several sets of aerial photographs, interviews, historical direct measurements, and state and federal government records to document long-term patterns.

Field and laboratory measurements

We used all 116 permanent plots to measure plant community characteristics and patterns in aboveground C over time. One plot (no. 213) was located very near the boundary of the land holding, and appeared to contain trees planted as part of a fence row. We measured soil C pools and C isotope values for this plot, but did not include the plant and soil data in our analyses of the regrowing forest (see section *Soil carbon pools and rates of accumulation*). We randomly selected 15 sample plots (hereafter called intensive study plots) for soil and litterfall measurements, controlling only for slope ($\leq 30\%$) and stratifying by species richness of trees >9.1 cm dbh (1992 values). We stratified by species richness to encompass a wide range in plant community structure. Selected plots contained a range of species richness from 4 to 16 species, with five plots each in low diversity (<7 species/plot), intermediate diversity (7–11 species/plot), and higher diversity (12–16 species/plot) classes. There was no evidence of recent disturbances (e.g., tree fall gaps, landslides) in the selected plots. A further subset of nine plots was selected for root sampling. These plots were selected such that three plots fell within each diversity category.

Plant community characteristics.—Using the data from the 115 plots, we calculated the basal area, stem density, species richness, and Shannon-Wiener diversity index (H') by plot (Pielou 1969, Krebs 1994). We also calculated the percentage of relative abundance, relative dominance, and frequency for each species. Importance values were determined by calculating the mean of the above three measures. We used species richness, defined as the number of species per plot, as the principal measure of species diversity. Species rich-

ness is conceptually simple, operationally feasible, and a widely reported measure of diversity (Magurran 1988, Hellman and Fowler 1999).

Soil carbon pools and rates of accumulation.—Forest floor samples (all recognizable, dead, organic material on the soil surface) were collected from 15×15 cm templates (inside area) at three locations in each of the intensive study plots. Sample locations were randomly selected along each of three, evenly spaced transects (10×1 m) radiating out from the plot center to ~ 1.5 m from the edge of the plot. We stratified the transects to assure plot coverage, and randomly located each sample along the transects. Forest floor samples were dried at 65°C , weighed to determine mass, and ground in a Cyclotec 1093 sample mill (Tecator, Eden Prairie, Minnesota, USA) to pass through a 1-mm mesh screen. Total C was measured on an elemental analyzer (CE Elantec, Incorporated, Lakewood, New Jersey, USA) at the University of California (U.C.), Berkeley, California, USA.

We used stable isotopes of C to determine the rates of soil C gain and loss relative to the previous land use. In the tropics, most pasture grasses use the C_4 photosynthetic pathway, while most forest trees use the C_3 pathway. Plants with the C_3 pathway discriminate against $^{13}\text{CO}_2$ during photosynthesis, causing the $^{13}\text{C}:^{12}\text{C}$ ratios of their phytomass to be depleted in ^{13}C (i.e., a more negative $\delta^{13}\text{C}$) relative to those of C_4 plants (Smith and Epstein 1971). The isotopic composition of soil organic C reflects the plant material from which it is derived, with relatively minor isotopic fractionation as it undergoes decomposition (Dzuresc et al. 1985). Therefore, the introduction of vegetation with a different dominant photosynthetic pathway provides an in situ label that allows us to approximate the net input rate of C from the new source.

Rates of soil C accumulation were determined in the 15 intensive study plots, three additional plots within the reforested area, and three sites in adjacent pasture in 1998–1999. The pasture (~ 3 ha) was at least as old as the forest, and may have been as much as 20 years older. The pasture was moderately grazed, and was never fertilized. We excavated one 50 cm ($n = 8$) to 60 cm ($n = 13$ including pasture sites) soil pit in each plot, and collected a quantitative soil core for C and bulk density estimations at 10 cm depth increments using a 6 cm diameter corer. There were no statistically significant differences in soil C pools or $\delta^{13}\text{C}$ between the 50 and 60 cm depths. Cores were taken ~ 5 cm back from the face of the pit in undisturbed, uncompacted soil. Cores were well mixed and subsampled for dry mass conversions at 105°C . Bulk density was calculated as the mass of oven-dry soil divided by the core volume.

Soils from each core were well mixed and ground to a fine powder for C analyses. Subsamples were tested with 5% HCl and showed no evidence of carbonates. Triplicate 45 mg subsamples were analyzed for $\delta^{13}\text{C}$

on an Europa 2020 continuous-flow mass spectrometer at U.C. Berkeley. The C isotope ratio was expressed in δ units relative to a PDB standard such that the $\delta^{13}\text{C} = (R_{\text{sa}} - R_{\text{st}}) \times 1000$, where R is the $^{13}\text{C}:^{12}\text{C}$ ratio of the sample (sa) and standard (st), respectively.

We estimated the proportion of C_3 - and C_4 -C in the samples using a modified version of the standard mixing equation proposed by Vitorello et al. (1989):

$$\begin{aligned} \%C_4 &= (\delta - \delta_L / \delta_G - \delta_L) \times 100 \\ \%C_3 &= 100 - \%C_4 \end{aligned} \quad (1)$$

where δ equals the $\delta^{13}\text{C}$ of the soil sample, δ_L is the $\delta^{13}\text{C}$ of a composite sample of forest floor and roots, and δ_G is a composite sample of pasture vegetation. Pasture vegetation averaged $-11.94 \pm 0.45\text{‰}$ ($n = 3$). The percentages of C_3 - and C_4 -C were then multiplied by the total C pool to estimate the proportion of C derived from the forest or pasture by depth. Values were corrected for bulk density by depth (Veldkamp 1994). We estimated a net rate of C sequestration or loss over time following reforestation as the difference between the C pools in the reforested sites and the adjacent pasture by depth.

Growth rates and aboveground C accumulation.— We calculated basal area increment from 1937 to 1959 and 1959 to 1992, and mortality rates from 1959 to 1992 using the subset of 426 trees that were measured in both surveys. These data are not expressed on a per hectare basis because only merchantable trees in the permanent plots were measured in 1959. We used the 1992 dataset of the 115 permanent plots to characterize the current plant community composition, aboveground biomass, and rates of aboveground C accumulation over the 55-year period from 1937 to 1992. On one hand, our growth rate data are conservative estimates because individuals were recruited into the stands over time. However, we also assumed that our sites contained no pre-existing trees for our C estimations. This is likely to lead to a slight overestimate in C pools because of the possibility of a small number of remnant trees on the site at the start of the reforestation effort. Aboveground biomass represents the net amount accumulated over the 55-year period. We calculated biomass using the following allometric equation from Brown (1997) for upland tropical forests:

$$Y = 21.297 - 6.953 \times \text{dbh} + 0.74 \times \text{dbh}^2 \quad (2)$$

where Y is in kilograms/tree and dbh is in cm. We chose this equation over other, similar equations using dbh because results most closely correlated with our estimates of volume based on basal area and height data. Height data were available for a subset of 196 trees. Species-specific allometric equations were not available for the majority of the species in the forest. One important potential source of error in our estimates and others that used stand-level allometric equations is that they do not consider differences in wood specific grav-

ity among species. The carbon content was assumed to be 50% of the biomass (Reichle et al. 1973).

Litterfall and fine-root biomass and productivity.— Litterfall was measured using five plastic litter collectors (0.14 m² each) in each plot ($n = 75$). One basket was randomly located in each of five equally spaced triangular subplots to assure plot coverage. Baskets were lined with mesh screening and suspended above the ground on polyvinyl chloride (PVC) poles to assure that litter did not come in contact with the soil. The bottoms of the baskets were perforated to avoid water pooling. Litter was collected monthly for two years (May 1996 through April 1998) and sorted into leaves, fine wood (≤ 7.5 cm diameter), fruits and flowers, and miscellaneous fractions. The fractions were dried at 65°C and weighed to determine mass.

We estimated changes in fine-root standing stocks over time in the 0–10 cm depth using the sequential coring technique (Vogt and Perrson 1991, Silver and Vogt 1993). Soil cores were sampled from five random locations in each plot ($n = 45$ /sampling period) every other month for one year (May 1997 through April 1998) using a root corer of 4.1 cm inside diameter. Cores were refrigerated until they were processed by sorting into live and dead pools by size class (≤ 2 mm diameter only) from washed sieves, generally within one to three months. Root samples were dried at 65°C and weighed to determine mass. We used the min-max technique to estimate rates of fine-root production among sampling dates; only dates where differences were statistically significant were used (Fairley and Alexander 1985, Vogt and Perrson 1991, Publicover and Vogt 1993). Estimating fine-root productivity is very difficult in tropical forests, and for this reason there are few root productivity data for these ecosystems. Problems arising from low sampling frequency and the lack of data on root decomposition are common and may apply here (Fairley and Alexander 1985). We present these data as a first approximation of belowground dynamics in a reforested tropical ecosystem, and to explore the potential effects of species composition and richness.

Statistical analyses

Statistical analyses were performed using Systat (Wilkinson 1990). We used simple and stepwise multiple linear regressions to determine the relationships among plant community structure, C pools, and rates of biomass or C accumulation. To examine differences in basal area and basal area increment between surveys, t tests were used. One-way and two-way analyses of variance (ANOVA) were used to determine if differences in C pools or rate processes occurred among treatments in relation to species dominance, species richness classes (low, medium, or high), or dates (litterfall and root biomass). Dominance was determined as $\geq 30\%$ of the plot basal area unless otherwise noted. Data were log-transformed when necessary to meet the

TABLE 2. The number of stems, relative dominance (RD), relative abundance (RA), frequency (F), importance value (IV), and basal area (BA) of the 40 most important tree species in the Cubuy Annex.

Species	No. stems	IV† (%)	RD (%)	RA (%)	F (%)	BA (m ² /ha)
<i>Tabebuia heterophylla</i>	1171	21.6	26.4	30.0	8.4	6.82
<i>Calophyllum antillanum</i>	293	6.3	7.4	7.5	4.1	1.90
<i>Andira inermis</i>	280	5.9	4.0	7.2	6.5	1.03
<i>Eugenia jambos</i>	303	5.5	4.8	7.8	3.9	1.23
<i>Hymenaea coubaril</i>	111	4.0	5.4	2.8	3.7	1.39
<i>Myrcia splendens</i>	127	3.5	1.3	3.3	5.9	0.33
<i>Guarea guidonia</i>	98	3.1	4.3	2.5	2.6	1.10
<i>Roystonea borinquena</i>	82	2.9	3.5	2.1	3.2	0.90
<i>Tectona grandis</i>	116	2.9	4.9	3.0	0.9	1.26
<i>Inga laurina</i>	79	2.5	2.6	2.0	2.8	0.67
<i>Mangifera indica</i>	68	2.3	2.9	1.7	2.3	0.76
<i>Ocotea leucoxylo</i>	81	2.1	1.4	2.1	2.8	0.35
<i>Swietenia macrophylla</i>	44	2.1	3.0	1.1	2.0	0.78
<i>Inga vera</i>	63	2.0	1.3	1.6	3.1	0.34
<i>Cupania americana</i>	55	1.9	1.3	1.4	2.9	0.33
<i>Ormosia krugii</i>	82	1.8	1.8	2.1	1.5	0.46
<i>Casearia guianensis</i>	59	1.7	0.8	1.5	2.8	0.20
<i>Guapira fragrans</i>	60	1.6	1.0	1.5	2.3	0.27
<i>Buchenavia tetraphylla</i>	25	1.6	2.7	0.6	1.4	0.71
<i>Cordia alliodora</i>	53	1.6	1.3	1.4	2.1	0.33
<i>Thespesia grandiflora</i>	44	1.4	1.2	1.1	1.9	0.31
<i>Cinamomum elongata</i>	22	1.3	2.5	0.6	0.9	0.64
<i>Schefflera morototoni</i>	40	1.3	1.1	1.0	1.7	0.27
<i>Casearia decandra</i>	48	1.2	0.5	1.2	1.9	0.12
<i>Zanthoxylum martinicense</i>	22	1.2	1.4	0.6	1.5	0.36
<i>Casearia arborea</i>	51	1.2	0.6	1.3	1.5	0.17
<i>Homalium racemosum</i>	42	1.1	0.7	1.1	1.5	0.17
<i>Dendropanax arboreus</i>	29	1.0	0.7	0.7	1.6	0.19
<i>Citharexylum fruticosum</i>	27	1.0	0.4	0.7	1.9	0.12
<i>Brysonima spicata</i>	24	0.9	1.1	0.6	1.0	0.28
<i>Casearia sylvestris</i>	28	0.8	0.3	0.7	1.5	0.07
<i>Beilschmiedia pendula</i>	25	0.8	0.4	0.6	1.5	0.09
<i>Cordia sulcata</i>	20	0.8	0.4	0.5	1.4	0.10
<i>Cecropia schreberiana</i>	13	0.7	0.8	0.3	0.9	0.20
<i>Ardisia obovata</i>	21	0.7	0.2	0.5	1.2	0.05
<i>Alchornea latifolia</i>	13	0.5	0.4	0.3	0.9	0.09
<i>Ocotea coriacea</i>	8	0.5	0.6	0.2	0.7	0.15
<i>Pisonia subcordata</i>	11	0.5	0.5	0.3	0.6	0.13
<i>Clusia clusioides</i>	11	0.4	0.5	0.3	0.5	0.13
<i>Coccoloba diversifolia</i>	13	0.4	0.2	0.3	0.7	0.06
Sum	3762	94.4	96.3	96.4	90.7	24.83

† IV = (RD + RA + F)/3.

assumptions for ANOVA. Pairwise comparisons using the Least Significant Differences (LSD) protocol were performed to determine where significant differences occurred. Residuals from all analyses were checked for normality and homogeneity of variances (Steel and Torrie 1980). We report significant differences at the 95% level unless otherwise noted. Values reported in text are means \pm 1 SE, unless noted otherwise.

RESULTS

Description of the reforested plant community

In 1992, there were 3903 trees and 75 tree species in the 115 permanent plots (4.6 ha), with 67 native species and eight nonnative species. Plot basal area varied from 8 to 55 m²/ha with a mean value of 26 ± 0.8 m²/ha. There were 2–17 species per plot (0.04 ha), with a mean of 9 ± 0.3 species; plot-level H' ranged

from 0.63 to 2.66 with a mean of 1.72 ± 0.04 . There was a mean of 8 ± 0.3 native species per plot, and the mean native plot level H' was 1.54 ± 0.04 . On average, there were 7 ± 3 species per plot that were not among those originally planted ($H' = 1.21 \pm 0.05$). Mean stem density was 840 ± 25 trees/ha.

There was high relative dominance and high relative abundance concentrated in a few species (Table 2). Approximately 49% of the relative dominance and 56% of the relative abundance was accounted for by five species (Table 2). *Tabebuia heterophylla* had the greatest importance value, relative abundance, and relative dominance. Of the 10 species with the highest importance values, only four were among those that were originally planted in the 1930s: *T. heterophylla*, *Calophyllum antillanum*, *Tectona grandis*, and *Hymenaea coubaril* (Table 2). These four species account for ~35% of the importance value in the reforested eco-

TABLE 3. Soil organic carbon (SOC, for C₃ and C₄) and total carbon (TC), by depth, for forest, pasture, and 61-yr-old reforested sites in the Cubuy Annex. Values are mean Mg C/ha (with 1 SE in parentheses).

Depth (cm)	Forest TC	Pasture			Reforestation			Net change†	
		TC	SOC ₄	SOC ₃	TC	SOC ₄	SOC ₃	SOC ₄	SOC ₃
10	30.9	30.2 (2.7)	25.3 (2.3)	4.9 (0.5)	42.8 (3.7)	6.8 (0.6)	36.0 (3.8)	-18.5	31.1
20	19.2	12.3 (1.9)	8.8 (1.4)	3.5 (0.5)	21.1 (1.5)	6.5 (0.5)	14.6 (1.2)	-2.3	11.1
30	15.0	8.7 (3.5)	5.5 (2.0)	3.2 (1.5)	13.6 (1.4)	5.1 (0.7)	8.5 (0.9)	-0.4	5.3
40	14.2	7.5 (3.1)	4.6 (1.7)	2.9 (1.4)	9.2 (1.2)	3.8 (0.6)	5.4 (0.6)	-0.8	2.5
50	19.7	5.0 (2.5)	3.2 (1.8)	1.8 (0.7)	8.5 (1.6)	3.5 (0.7)	5.0 (0.9)	0.3	3.2
60	...	5.0 (2.1)	3.3 (1.6)	1.7 (0.5)	7.2 (2.3)	2.6 (1.1)	4.5 (1.2)	-0.7	2.8

Note: Sample sizes: $n = 10$ pits for the reforested sites, and $n = 3$ pits for the pasture sites.

† The net change in soil C pools is calculated as the difference between the pasture and reforested sites.

system. Planted nonnative species accounted for only 5% of the importance value.

Soil C pools and rates of soil C accumulation and loss

The forest floor C pool was 4.3 ± 0.4 Mg/ha, and did not vary significantly with any plant community characteristics (data not shown). There was 102 ± 10 Mg/ha of C in the top 60 cm of soil of the reforested plots ($n = 10$ pits), and the soil C content decreased with depth in the top 30 cm of mineral soil (Table 3). The soil C pool was significantly positively correlated with the combination of forest floor C and the basal area of *Mangifera indica*, a nonnative fruit tree used locally in gardens ($r^2 = 0.60$, $P < 0.01$, $n = 15$). It is possible that one or a few individuals of *M. indica* were pre-existing on the site as garden or shade trees; however, comparisons of median dbh (17.4 cm) and the range in dbh (80 cm, $n = 68$) for *M. indica* were similar to several non-garden tree species that were likely to have naturally colonized the site after planting, such

as *Guarea guidonia* (median dbh = 17.4 cm, range = 80 cm, $n = 98$), *Cinamomum elongatum* (median dbh = 34.5 cm, range = 95 cm, $n = 22$), and *Buchenavia tetraphylla* (median dbh = 37.5 cm, range = 67 cm, $n = 25$). Therefore, the profuse litter production of *M. indica* is likely to be responsible for the relationship. Pasture soils had significantly lower soil C than the reforested soils ($P = 0.05$), most notably in the 0–20 cm depth (Table 3).

There was an average $4.2 \pm 0.3\%$ shift in the $\delta^{13}\text{C}$ of soil organic matter with depth (Fig. 1, Table 4), and a maximum range of -28% in surface soils to -19% at depth in the reforested plots. In one plot (no. 213) there was essentially no change in the C isotope ratio with depth ($-26.4 \pm 0.2\%$). This plot was located very near the boundary of the Cubuy Annex and adjacent to a path through the forest. We suspect that this plot may have not been in pasture, and likely consisted of planted trees that were part of a fencerow or windrow on the edge of the pasture. We refer to this site as the “forested” site for comparison purposes, and exclude it from the reforested group for soil and plant analyses. In the reforested sites, the least negative $\delta^{13}\text{C}$ values occurred at depths of 30–50 cm ($-22.4 \pm 0.3\%$). At these depths, the C₄-C amounted to $39 \pm 2\%$ of the total C pool. The pasture soils had less negative $\delta^{13}\text{C}$ values ranging from -15% to -20% . The pasture soils ranged from 60% to 83% C₄-C, with the greatest quantity in the 0–10 cm depth, and the least amount in the 50–60 cm depth (Table 4).

We compared the C pools in the reforested sites with the adjacent pasture to determine the net change in soil C by depth with reforestation (Table 3). There was a total net gain of 33 Mg C/ha in the reforested sites with 64% accumulating in the top 20 cm of mineral soil. The total C₃-C sequestered was 56 Mg/ha, but this amount was offset by the loss of 23 Mg/ha from the C₄-C pool. The greatest loss of C₄-C came from the 0–10 cm depth (-19 Mg/ha), which was coupled with a gain of C₃-C of 31 Mg/ha. The rate of change in the soil C₃- and C₄-C pools with reforestation can be roughly calculated as the sum of C₃- or C₄-C added or lost throughout the profile, after correction for the percentage of C₃- and C₄-C in the pasture, divided by the

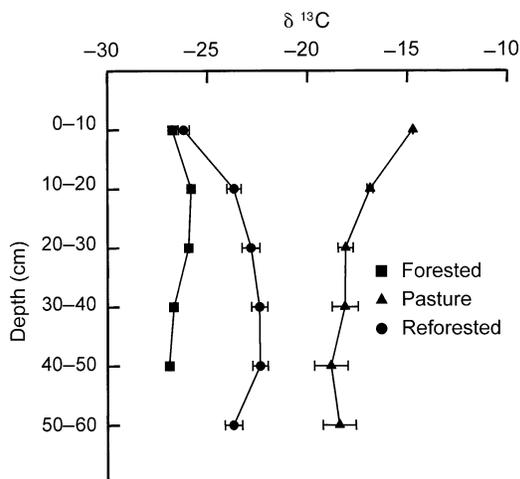


FIG. 1. The ^{13}C of soil organic matter (mean \pm 1 SE) by depth in 61-yr-old reforested plots, one forested site, and an adjacent pasture in the Cubuy Annex of the Luquillo Experimental Forest, Puerto Rico. For the 0–50 cm depth, $n = 18$ reforested plots, and $n = 3$ pasture plots. For the 50–60 cm depth, $n = 10$ reforested plots, and $n = 3$ pasture plots.

TABLE 4. Delta ^{13}C of soil, by depth, from forest, pasture, and 61-yr-old reforested sites and SOC_4 and SOC_3 (%) by depth in pasture and reforested sites in the Cubuy Annex. Values for the reforested and pasture sites are means (with 1 SE reported in parentheses).

Depth (cm)	Forest ^{13}C (‰)	Pasture			Reforestation		
		^{13}C (‰)	SOC_4 (%)	SOC_3 (%)	^{13}C (‰)	SOC_4 (%)	SOC_3 (%)
10	-26.76	-14.72 (0.01)	83	16 (0)	-26.18 (0.28)	29	71 (1)
20	-25.81	-16.87 (0.15)	71	29 (1)	-23.67 (0.35)	42	58 (2)
30	-25.94	-18.10 (0.38)	64	36 (2)	-22.83 (0.44)	46	54 (2)
40	-26.69	-18.13 (0.65)	64	36 (4)	-22.40 (0.40)	48	52 (2)
50	-26.92	-18.83 (0.83)	60	40 (5)	-22.39 (0.39)	48	52 (2)
60	...	-18.42 (0.83)	62	38 (5)	-23.70 (0.43)	41	59 (2)

Note: Sample sizes: $n = 10$ pits for the reforested sites, and $n = 3$ pits for the pasture sites.

time in years. This gives a rate of soil $\text{C}_3\text{-C}$ sequestration of $0.90 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and a rate of loss of $\text{C}_4\text{-C}$ of $0.36 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. The net rate of soil C accumulation was $0.54 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for the soil profile. These values are estimates because there may have been concomitant $\text{C}_3\text{-C}$ loss from the pasture sites from the residual forest C stock, particularly from the bottom of the soil profile (resulting in a slight overestimate). There were no patterns in the rate of soil C accumulation by species composition, richness, Shannon-Weiner diversity, or dominance.

Aboveground C content and growth rates

There was $80 \pm 3 \text{ Mg C/ha}$ in the aboveground biomass in the reforested ecosystem ($n = 115$). The rate of aboveground C accumulation for the 55-year period from 1937 to 1992 was $1.4 \pm 0.05 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. There were no significant relationships among diversity or dominance and rates of aboveground C accumulation. The sum of aboveground, forest floor, and soil (0–50 cm) C pools in the intensively sampled plots was $195 \pm 14 \text{ Mg/ha}$.

Because species-specific allometric equations did not exist for the majority of the 75 tree species at this site, we used basal area as a means to examine trends in the size and growth rate of important species. There were no statistically significant differences among the top 10 species with regard to mean basal area and basal area increment. *Cinamomum elongatum* had the greatest average basal area ($3.33 \pm 0.92 \text{ m}^2/\text{ha}$, $n = 22$) followed by *Buchenavia tetraphylla* ($3.26 \pm 0.53 \text{ m}^2/\text{ha}$, $n = 29$), both native species. Of the planted species, *S. macrophylla*, *H. coubaril*, and *Brysonima spicata* were among the 10 largest tree species. *Tabebuia heterophylla* and *C. antillanum* ranked 23rd and 18th, respectively.

Merchantable trees measured in 1959 and 1992.—Twenty-one species were included in both surveys (Table 5). Seven species had the greatest annual basal area increment ($24\text{--}40 \text{ cm}^2/\text{yr}$) during the 1959 to 1992 period, and were not statistically distinguishable from one another. These included three timber species (*T. grandis*, *S. macrophylla*, and *Guarea guidonia*), one early successional tree species (*Cecropia schreberiana*), and

three other native species (*B. tetraphylla*, *C. antillanum*, and *Zanthoxylum matrinicense*). Among the slow-growing species were the dominant tree species *T. heterophylla*, as well as the early-successional species *Schefflera morototoni*.

Overall, merchantable tree species grew faster in the second 33-year period than in the initial 22 years ($P < 0.01$), and there were large differences in the basal area increment by tree species (Table 5). *Buchenavia tetraphylla* had the greatest diameter growth rate during both measurement periods. *Swietenia macrophylla* had the greatest increase in growth rate ($29.8 \text{ cm}^2/\text{yr}$) from the first to the second growth period. *Tabebuia heterophylla* showed no significant increase in growth rate, while *C. antillanum* showed a large increase ($14.5 \text{ cm}^2/\text{yr}$). There was a weak positive relationship between the basal area in 1959 and growth rate over the subsequent 33 years ($r^2 = 0.13$, $P < 0.01$, $n = 426$).

Sixteen trees died over the 33-year period from 1959 to 1992, yielding a mean mortality rate of 3.7% (0.1% annually). The native species *C. elongatum* suffered the highest mortality rate among species (27%, $n = 15$), while only four of 266 tagged individuals of *T. heterophylla* died between the two sampling periods.

Litterfall and fine-root production and rates of biomass accumulation litterfall.—There was significantly more total annual litterfall in the first year ($12.9 \pm 0.5 \text{ Mg/ha}$) than in the second year ($10.6 \pm 0.5 \text{ Mg/ha}$) of measurement, due primarily to the input from two tropical storms in July and September 1996 (Figs. 2 and 3). The two storms resulted in approximately equal amounts of litter inputs ($3.1 \pm 0.3 \text{ Mg/ha}$), and together accounted for one-third of the total non-storm annual litterfall.

Litterfall showed several patterns with plant community structure over the two years of measurement. During the first year, total annual leaf fall was weakly positively correlated with stem density ($r^2 = 0.29$, $P < 0.04$, $n = 15$). There were no significant effects of relative dominance, species richness, or Shannon-Weiner diversity on monthly litterfall fractions or total monthly or annual litterfall. Plots dominated by *T. heterophylla* ($\geq 30\%$ of the basal area, $n = 7$) had significantly less total litterfall ($P < 0.05$) than other plots

TABLE 5. Mean (with 1 SE in parentheses) basal area increment (cm^2/yr) in merchantable tree species from 1937 to 1959, 1959 to 1992, and over the entire 55-year period from 1937 to 1992 in the Cubuy Annex.

Species	<i>n</i>	1937–1959	1959–1992	1937–1992
<i>Tabebuia heterophylla</i>	265	8.3 (0.4)	8.4 (0.5)	8.4 (0.3)
<i>Calophyllum antillanum</i>	22	9.7 (1.2)	24.2* (3.5)	18.4 (2.4)
<i>Ormosia krugii</i>	22	7.0 (1.0)	8.6 (1.2)	8.0 (0.9)
<i>Buchenavia tetraphylla</i>	18	29.9 (5.6)	39.7* (6.6)	35.8 (4.9)
<i>Cinamomum elongata</i>	15	17.9 (3.0)	19.1 (3.3)	18.6 (2.4)
<i>Inga laurina</i>	13	10.7 (2.5)	20.2* (3.5)	16.4 (2.7)
<i>Swietenia macrophylla</i>	11	10.6 (2.7)	40.4* (6.9)	28.5 (4.6)
<i>Guarea guidonia</i>	8	16.3 (4.1)	24.9* (5.4)	21.4 (4.0)
<i>Tectona grandis</i>	7	17.2 (2.4)	18.3 (2.1)	17.9 (1.7)
<i>Ocotea leucoxydon</i>	7	6.8 (0.9)	12.3 (2.6)	10.1 (1.5)
<i>Zanthoxylum martinicense</i>	7	9.2 (2.3)	27.9* (6.7)	20.4 (4.6)
<i>Brysonima coriacea</i>	6	12.6 (1.0)	13.6 (3.0)	13.2 (1.7)
<i>Schefflera morototoni</i>	5	8.4 (1.8)	7.3 (3.5)	7.7 (1.7)
<i>Cordia alliodora</i>	5	9.0 (2.9)	10.2 (2.9)	9.7 (1.5)
<i>Homalium racemosum</i>	4	5.3 (0.3)	9.6 (3.6)	7.9 (2.2)
<i>Alchornea latifolia</i>	3	11.6 (2.4)	18.9 (13.4)	16.0 (7.8)
<i>Cecropia schreberiana</i>	3	11.9 (1.2)	31.2 (6.3)	23.5 (3.6)
<i>Linociera domingensis</i>	2	10.5 (4.9)	4.9 (2.9)	7.2 (3.7)
<i>Meliosma herbertii</i>	1	4.2	5.0	4.7
<i>Dacryodes excelsa</i>	1	32.1	16.3	22.6
<i>Petitia domingensis</i>	1	3.6	14.5	10.1

Notes: Asterisks signify statistically significant differences between the first two measurement periods ($P < 0.05$). Only species with >3 individuals were tested.

($n = 8$). Plant community effects were also apparent in response to the two tropical storms. Total litterfall inputs for the July storm were significantly positively correlated with plot basal area ($r^2 = 0.41$, $P < 0.01$). Fruit and flower inputs from the September storm were positively correlated with the basal area of *C. antillanum* ($r^2 = 0.30$, $P < 0.05$), and the combination of plot-level stem density and *C. antillanum* basal area (r^2

$= 0.42$, $P < 0.05$). The proportion of annual inputs from the two storms combined was positively correlated with the number of *T. heterophylla* stems ($r^2 = 0.47$, $P < 0.01$). The relationship improves when the number of *C. antillanum* stems are added ($r^2 = 0.60$, $P < 0.01$).

Fine-root biomass and productivity.—Total fine-root biomass in the reforested plots was 2.5 ± 0.1 Mg/ha. There was significantly more dead-root biomass (2.3 ± 0.1 Mg/ha) than live root biomass (0.1 ± 0.02 Mg/ha). Live root biomass differed significantly ($P < 0.05$) over time (Fig. 4); lower live root biomass was measured in October 1996, December 1996, and April 1997. Dead-root biomass also appeared to be lower in October 1996 and December 1996, but the differences were not statistically significant at the 95% level. Total fine-root standing stocks were significantly greater ($P < 0.05$) in plots dominated by *C. antillanum* (2.9 ± 0.2 Mg/ha, $n = 3$) than in plots dominated by other species combined (2.1 ± 0.1 Mg/ha, $n = 4$). Mean fine-root productivity was 0.29 ± 0.09 Mg·ha⁻¹·yr⁻¹ ($n = 9$ plots), and showed no trends with forest community structure or composition.

DISCUSSION

Reforestation for biodiversity and C sequestration: Do planted species persist?

Reforestation resulted in a large increase in biodiversity over 55 years, although many of the common species were part of the original planting effort. Most of the species planted in 1937 persisted, but only four could be considered dominants, and of those, one species contributed 26% to the relative dominance and the

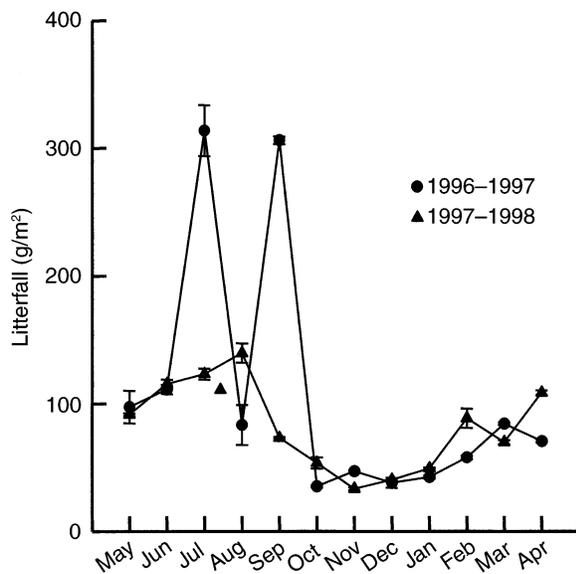


FIG. 2. Monthly litterfall (mean \pm 1 SE) in 61-yr-old reforested plots of the Cubuy Annex ($n = 15$ plots and 75 baskets/mo). Year 1 (circles) was May 1996–April 1997, and year 2 (triangles) was May 1997–April 1998.

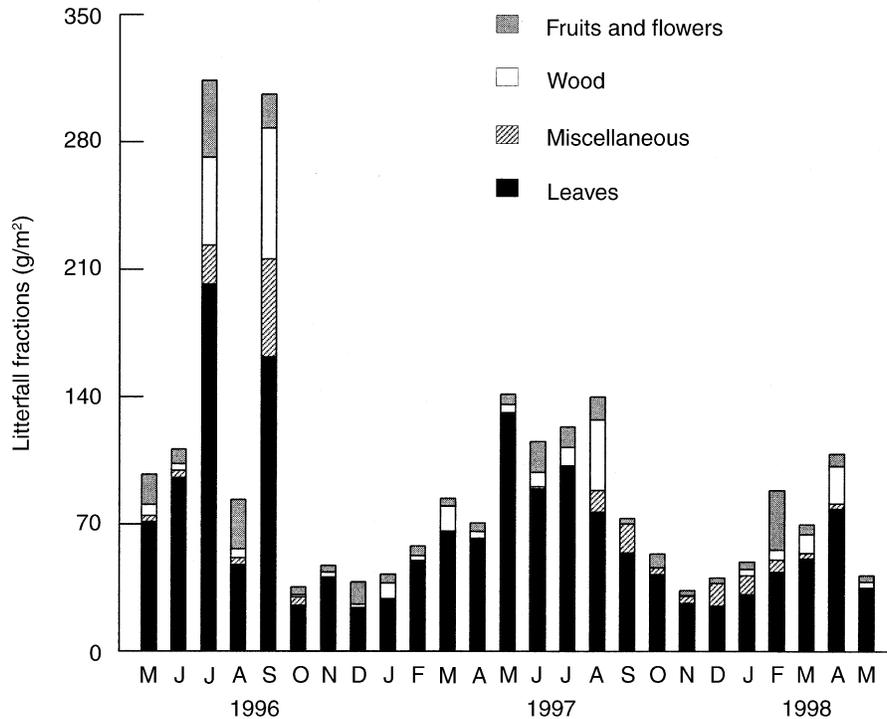


FIG. 3. Mean monthly litterfall fractions in 61-yr-old reforested plots of the Cubuy Annex from May 1996 to May 1998.

other three species combined contributed only 17%. Only one of these species, *T. grandis*, was not native. *Tabebuia heterophylla* was by far the most abundant species, and had the greatest importance value. *T. heterophylla* produces wind-dispersed seeds and is generally considered an early-successional species that grows well on most soils types, including degraded soils. It is widely planted as a timber tree and in gardens

for ornamentation, and commonly establishes in heavily grazed pastures (Marrero 1947). Therefore, it is likely to have recruited naturally in addition to being planted, accounting for its strong dominance in the restored forest.

Of the four nonnative species that were planted in the 1930s, three were still present in 1992 (teak, big-leaf mahogany, and *Swietenia mahogoni*), although there was only one remaining individual of *S. mahogoni* in the surveyed plots. Teak had high relative dominance and abundance, but low frequency, suggesting that it was not widely planted, did not successfully establish widely when planted, and/or has not dispersed much throughout the study area. In this ecosystem, teak reproduces primarily through vegetative sprouting, which slows the rate of spread over large areas. Mahogany had low relative abundance in 1992, but high mean basal area and intermediate frequency. Escaped garden and shade trees also left an imprint on the landscape. The nonnative species *E. jambos* and *M. indica*, and the native species *Inga laurina* and *I. vera*, ranked 4th, 11th, 10th, and 14th in importance value, respectively. *I. vera* is often planted as coffee shade, and *I. laurina* produces an edible fruit. There are no records that *Inga* spp. were planted at the site, so they probably colonized from nearby coffee plantations.

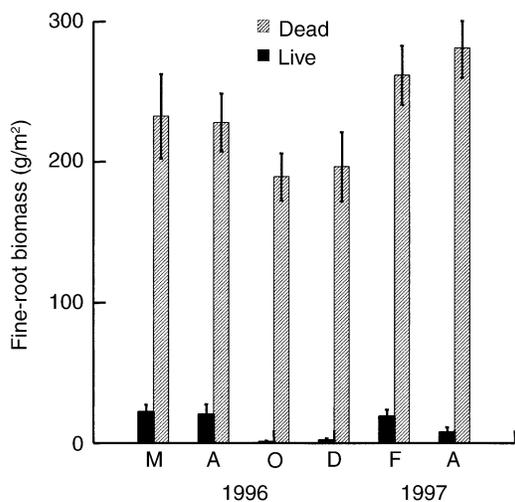


FIG. 4. Live and dead fine-root biomass (mean \pm 1 SE) in 61-yr-old reforested plots of the Cubuy Annex ($n = 9$ plots). Some samples were lost during transport from May 1996 [$n = 4$ plots] and December 1996 [$n = 7$ plots].

The pasture legacy and soil carbon sequestration

Several studies have measured soil C pools following tropical forest regrowth (Weaver et al. 1987, Busch-

bacher et al. 1988, Brown and Lugo 1990b, Cuevas et al. 1991, Reiners et al. 1994, Hughes et al. 1999), but because they measured bulk soil C content and did not differentiate between the sources from which the C was derived, it is difficult to tell how much new C is gained, and how much of the previous C was retained or lost. Using stable C isotopes, Bashkin and Binkley (1998) and Binkley and Resh (1999) found that afforestation with Eucalyptus in Hawaii resulted in only small net gains in soil C in the surface soils in young stands (≤ 13 years old) because of relatively large losses of C from the residual land use. Similarly, rates of C_3 -C gain were significantly offset by C_4 -C loss in 20-year-old second growth in Ecuador (Rhoades et al. 2000).

In this study, 61 years following the conversion of pasture to forest, there was still 28 Mg C_4 -C/ha; $\sim 28\%$ of the total soil C pool to 60 cm depth. There was a gain of 56 Mg C_3 -C/ha in the top 60 cm of mineral soil, but a corresponding loss of 23 Mg C_4 -C/ha, yielding a net gain of 33 Mg/ha. The net rate of soil C sequestration was ~ 0.5 Mg·ha $^{-1}$ ·yr $^{-1}$, considerably slower than the rate of C_3 -C added to the soil (0.9 Mg·ha $^{-1}$ ·yr $^{-1}$). This rate of soil C sequestration is similar to rates (not considering losses) reported for natural secondary succession in tropical moist forests (0.5 Mg·ha $^{-1}$ ·yr $^{-1}$, Brown and Lugo 1990b; 0.7 Mg·ha $^{-1}$ ·yr $^{-1}$, Post and Kwon 2000), and at the lower end of the range reported for 50-year-old secondary forests in Puerto Rico (0.8–4 Mg·ha $^{-1}$ ·yr $^{-1}$, Lugo et al. 1986). In a pantropical survey, Silver et al. (2000b) reported a soil C accumulation rate of 0.49 Mg·ha $^{-1}$ ·yr $^{-1}$ following pasture abandonment in the top 25 cm of mineral soil, and an overall rate of 0.41 Mg·ha $^{-1}$ ·yr $^{-1}$ during the first 100 years of forest regrowth following all land uses. These results together with those reported here suggest that soil C accumulates more slowly than aboveground C, but that significant soil C sequestration can occur with reforestation of pasture over time, even in the later stages of succession.

Aboveground carbon pools and rates of carbon accumulation following reforestation

The forest accumulated aboveground C at a rate of 1.4 Mg·ha $^{-1}$ ·yr $^{-1}$ since establishment in the 1930s. This rate is lower than rates reported for young (0–20 years) secondary forests (Brown and Lugo 1990a), at the low end of rates measured in young tropical plantations (Brown et al. 1986), and intermediate in comparison to older (60–80 years), intact and logged tropical forests (Lugo and Brown 1992). Saldarriaga et al. (1988) found similar rates of aboveground C accumulation (1.5 ± 0.3 Mg C·ha $^{-1}$ ·yr $^{-1}$) in 60-year-old secondary forests recovering from slash and burn agriculture in northern South America. The relatively slow growth rate of the forest may be due to degradation at the site prior to forest establishment. However, the 55-year-old forest was accumulating C at a faster rate than more

mature systems. A recent estimate of the rate of C sequestration by old-growth humid tropical forest biomass was $\sim 0.53 \pm 0.26$ Mg C·ha $^{-1}$ ·yr $^{-1}$ (Phillips et al. 1998), approximately one-third of the rate measured here.

Lugo and Brown (1992) reported that a large proportion of the net accumulation of aboveground biomass in tropical forests occurs as continued growth of large trees as opposed to ingrowth of smaller individuals. If we define large trees as having a dbh ≥ 25 cm, then 16% of the stems accounted for $>50\%$ of the total aboveground C pool. While planted species dominated the reforested ecosystem, they were not necessarily the fastest growing species. Only three planted species were among the 10 species with the greatest annual basal area increment.

Most studies calculate growth rates based on one measurement interval in tropical forests. Here we found that stem growth rates differed depending upon the time period used. The mean basal area increment in individual trees increased from 10 cm 2 /yr during the first 22 years of stand development to 14 cm 2 /yr during the subsequent 33-year period. This may be due to factors such as changes in soil and microclimatic conditions as the canopy closed, neither of which was measured in the late 1950s. Initial growth rates may have been slow due to factors such as competition from pasture grasses, low nutrient availability, or drought stress in a degraded ecosystem. The increase in growth rate presents some interesting issues with regards to estimates of stand development. Most studies have focused on the first 10 to 20 years of growth following disturbance, reforestation, or afforestation (Lugo and Brown 1992). Using the early growth estimate to extrapolate to the long-term potential of reforested ecosystems for C gain may significantly underestimate this potential. The average basal area increment also differed by species. *Buchenavia tetraphylla* was abundant and had a high initial growth rate, approximately twice as fast as the next fastest growing species. *Buchenavia tetraphylla* also had the highest growth rates for the second measurement period. The most common species, *T. heterophylla*, grew much more slowly during both measurement periods, suggesting that it may sacrifice high-sustained growth rates for successful establishment, high fecundity, and high survival rates. Growth rates are likely to represent the high end of the range among all species because this analysis only considered merchantable trees.

Carbon transfers in litterfall and fine roots

Above- and belowground litter production are important components of C cycling and are one indicator of ecosystem functioning following restoration or reforestation (Ewel 1987, Silver et al. 1996). Litterfall rates were high in the reforested sites compared with nearby young secondary forests, but lower than nearby pine plantations in the same life zone (Lugo 1992). A

recent pantropical review of tropical forest litterfall rates reported a range from 1.8 to 11.8 Mg·ha⁻¹·yr⁻¹, with an average of 6 ± 0.4 Mg·ha⁻¹·yr⁻¹ (Clark et al. 2001). This, too, is low compared to the 10–12 Mg·ha⁻¹·yr⁻¹ measured here. Litterfall inputs increased significantly in response to two tropical storms that hit the forest in 1996, but appeared to return to pre-storm values very quickly. Tropical storms are a common annual occurrence in the Caribbean (Larsen and Scatena 1991). Damage from tropical storms generally consists of increased fine litterfall inputs, possible branch falls, and isolated treefalls or landslides, and is much less severe than the widespread and catastrophic destruction associated with less frequent hurricanes (Walker et al. 1991). This type of periodic non-catastrophic disturbance is typical of Caribbean ecosystems (Lugo and Waide 1993), and species in the reforested plots appear to be well adapted to these events.

Very few studies have measured fine-root biomass following reforestation in the tropics, and even fewer have measured fine-root dynamics. Sixty-one years of reforestation resulted in fine-root standing stocks that were similar to values reported for old growth lower montane tropical forests (Cavelier 1992, Silver and Vogt 1993), and lower than values reported for young secondary forests (Cuevas et al. 1991). Plantation species are often chosen for their ability to produce wood products, and thus may allocate proportionally more C aboveground (particularly to wood) than belowground when compared with natural secondary forest species (Lugo 1992). Here, plots dominated by one timber species, *C. antillanum*, showed relatively high fine-root biomass.

The effects of reforestation on ecosystem carbon pools and rates of change

One of the goals of this study was to determine if biodiversity, plant community structure, or species composition influenced above- or belowground C pools or dynamics. Linkages between indices of biodiversity and ecosystem processes are extremely difficult to establish in natural ecosystems, and are likely to be particularly hard to detect in relatively diverse ecosystems such as tropical forests (Silver et al. 1996). We found that the diversity, degree of dominance, or composition had few discernable impacts on aboveground C pools or rate of aboveground C accumulation. Furthermore, there was little indication that the composition or structure of the plant community affected rates of soil C accumulation or the size of the soil C pool. Even in the “low diversity” plots, one might not expect to see an effect of diversity or species composition unless a particular species displayed a trait (e.g., N fixation, crassulacean acid metabolism [CAM], or C₄ photosynthesis/high water use efficiency) that would impose a discernable effect on ecosystem processes (Chapin et al. 1995). Here, there were few obvious traits that could impose a discernable effect on the processes we mea-

sured. The most obvious effect was that the size of the soil C pool was positively correlated with the basal area of *M. indica* (mango) and forest floor C. Mango produces prolific litter with several leaf flushes throughout the year, leading to high litterfall inputs to the forest floor. The presence of a N-fixing species, *I. vera*, had no measurable impact on above- or below-ground productivity or C pools. This is likely to be due to relatively high mineral N availability typical of volcanically derived old tropical forest soils (Vitousek and Sanford 1986).

We were able to detect significant effects of species composition and dominance on the amount and distribution of litter inputs across the landscape, but no patterns emerged for species richness or Shannon-Weiner diversity. Strong basal area dominance by *T. heterophylla* resulted in lower annual litterfall than in other plots. As mentioned above, this is a slow-growing species, can become semi-deciduous, and may retain its leaves for multiple years (Weaver 1990).

CONCLUSIONS

Our results reveal that significant C sequestration can occur in older reforested and afforested ecosystems in the tropics. The majority of research on C dynamics of regrowing tropical forests has concentrated on the first 20 years when tree growth rates are assumed to be at a maximum. Here we found that trees exhibited greater rates of C sequestration during the later 33 years of growth, as opposed to the first 22 years. We also found significant C sequestration in soils in old reforested sites, even after accounting for the loss of residual soil C from the previous land use. This is a particularly important finding, as many studies have assumed that conversion of pasture to forest will result in a net loss of C from soil. These results have important implications for C offset programs. The maintenance of older reforested or afforested sites (as opposed to short-rotation systems) can yield significant C sequestration in long-term storage pools such as wood and soil organic matter. Our results also highlight the value of reforestation for augmenting biodiversity, and suggest that, at least in our sites, the use of nonnative species does not have significant negative consequences for the re-establishment of native plant communities. Reforestation of abandoned and degraded tropical lands has great potential to increase rates of C sequestration from the atmosphere and enhance biodiversity. The magnitude of this potential has not been widely quantified, but is important for the development of management strategies, and in setting national and international policy.

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