

LONG-TERM PATTERNS IN TROPICAL REFORESTATION: PLANT COMMUNITY COMPOSITION AND ABOVEGROUND BIOMASS ACCUMULATION

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Abstract. Primary tropical forests are renowned for their high biodiversity and carbon storage, and considerable research has documented both species and carbon losses with deforestation and agricultural land uses. Economic drivers are now leading to the abandonment of agricultural lands, and the area in secondary forests is increasing. We know little about how long it takes for these ecosystems to achieve the structural and compositional characteristics of primary forests. In this study, we examine changes in plant species composition and aboveground biomass during eight decades of tropical secondary succession in Puerto Rico, and compare these patterns with primary forests. Using a well-replicated chronosequence approach, we sampled primary forests and secondary forests established 10, 20, 30, 60, and 80 years ago on abandoned pastures. Tree species composition in all secondary forests was different from that of primary forests and could be divided into early (10-, 20-, and 30-year) vs. late (60- and 80-year) successional phases. The highest rates of aboveground biomass accumulation occurred in the first 20 years, with rates of C sequestration peaking at $6.7 \pm 0.5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Reforestation of pastures resulted in an accumulation of 125 Mg C/ha in aboveground standing live biomass over 80 years. The 80 year-old secondary forests had greater biomass than the primary forests, due to the replacement of woody species by palms in the primary forests. Our results show that these new ecosystems have different species composition, but similar species richness, and significant potential for carbon sequestration, compared to remnant primary forests.

Key words: *abandoned pastures; biomass; carbon; Prestoea acuminata var. montana; Puerto Rico; reforestation; secondary forests; secondary succession; Syzygium jambos; Tabebuia heterophylla; tropical forests.*

INTRODUCTION

Secondary forests are the dominant forest cover type in the tropics (Brown and Lugo 1990, Houghton 1994). Although these ecosystems are often undervalued, tropical secondary forests can provide some of the same important ecosystem goods and services as primary forests, such as watershed protection, erosion control, regional climate stabilization, wood and non-timber products, and habitat for biodiversity (Brown and Lugo 1990, Guariguata and Ostertag 2001, Naughton-Treves and Chapman 2002). Shifts from agrarian to industrial economies and associated urban and international migration has led to widespread abandonment of agricultural and pasture lands and increasing rates of natural reforestation in tropical countries (Rudel et al. 2002, Aide and Grau 2004, Arroyo-Mora et al. 2005). The success and rates of reforestation on abandoned fields and pastures at the regional scale depend on the

method of clearing (Uhl et al. 1988, Chinea 2002), the type and intensity of the previous land use (Nepstad et al. 1991, Aide et al. 2000, Moran et al. 2000), frequency of fire (Zarin et al. 2005), availability of seed sources and dispersers (Duncan and Chapman 1991, Holl et al. 2000), and competition by other land uses such as residential or commercial development (Thomlinson et al. 1996).

Species composition, structure, and dynamics of secondary forests are influenced by past land-use history and disturbance (García-Montiel and Scatena 1994, Foster et al. 1999, Aide et al. 2000, Caspersen et al. 2000, Moran et al. 2000, Chazdon 2003). Historical land use can embark secondary forests on a new successional trajectory (Lugo and Helmer 2004). These ecosystems have been called “novel” or new forests as they consist of a mix of old and new components (Lugo and Helmer 2004, Hobbs et al. 2006). The legacy of land-use change can persist in the plant community, even in ecosystems that experience frequent or catastrophic disturbances (Zimmerman et al. 1995, Boucher et al. 2001, Thompson et al. 2002, Pascarella et al. 2004).

Reforestation of abandoned agricultural and pasturelands in the tropics has been proposed by the

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Intergovernmental Panel on Climate Change as a strategy to increase C sequestration in terrestrial ecosystems and help mitigate anthropogenic C emissions (Brown et al. 1996, Metz et al. 2001). Reforestation provides the opportunity for ecosystems to recover function and biodiversity and serve as potential sinks for atmospheric C in both plant biomass and soil organic matter (Lugo and Brown 1992, Silver et al. 2000, Lamb et al. 2005). Most research on biomass and C accumulation rates in tropical secondary forests has focused on the first 20 years of forest regrowth (Silver et al. 2000). We have a limited understanding of the longer-term behavior of secondary forests as potential C sinks.

This study takes advantage of a historical trend in natural reforestation of abandoned pastures in Puerto Rico to study the dynamics of forest structure, species composition, and aboveground biomass during eight decades of secondary succession. Our goals were to determine the long-term potential of recovering forests to sequester C in aboveground biomass and their conservation value for tree biodiversity. The availability of a large number of sites more than 20 years old allowed us to determine the value of secondary forest as a long-term land-cover type in the tropics.

METHODS

Land-use change in Puerto Rico

The Caribbean island of Puerto Rico is an ideal case study for examining the effects of land-use change because of the availability of historical records, aerial photographs, and long-term data sets that facilitate chronological documentation of land-cover change, as well as an established history of long-term ecological research. The mountainous regions of Puerto Rico represent a shifting mosaic of land uses due to the typically small size of land holdings and multiple cycles of human migration, which lead to a network of patches of land in different stages of cultivation or abandonment (Thomlinson et al. 1996, Helmer 2004).

Widespread deforestation occurred in the 19th century concurrent with a large influx of people to the island (Domínguez Cristóbal 2000). In the 1820s, pastures covered approximately 55% of the island (Wadsworth 1950). In 1900, more than three-quarters of the island was deforested, with about 78% of the land surface under agricultural or livestock use, primarily as sugar cane, coffee, and pastures (Wadsworth 1950). Major political and socioeconomic changes, starting in the late 1940s, resulted in large-scale agricultural abandonment as the economy shifted to light industry and services, and as human populations migrated from rural areas to urban centers and to the continental United States (Dietz 1986). Agricultural abandonment led to an island-wide increase in forest cover (Franco et al. 1997, Grau et al. 2003). In the mid-1940s, it is estimated that only about 13% of Puerto Rico's area was covered by closed forest (Weaver and Birdsey 1990). The percentage of forested land increased to 30% in 1980 and 34% in

1985. In 1991–1992, dense forest covered 41.6% of the main island (Helmer et al. 2002). The Sierra de Cayey region, where our study sites are located, experienced a three-fold increase in forest cover from 1937 to 1995 (Pascarella et al. 2000). The increase in forests from less than 20% to 62% in a 60-year period was concurrent with a decrease in pasture cover from almost 50% of the area to less than 20%. Similar trends in reforestation of formerly cultivated and grazed lands have been reported for other regions across the tropics (Aide and Grau 2004).

Site description

We conducted this study on private land near the border between the municipalities of Guayama and Patillas in the Sierra de Cayey in southeastern Puerto Rico (18°01' N, 66°05' W). The sites were located between 580 and 700 m above sea level in the subtropical wet forest life zone (Ewel and Whitmore 1973). The potential forest vegetation types in the region are lower montane wet evergreen forest, tall cloud forest (as evidenced by the presence of epiphytic bromeliads near the ground) and palm breaks (Helmer et al. 2002). The dominant soil type in this region is classified as very fine, mixed, isothermic, Inceptic Hapludox in the Los Guineos series (Lugo-López et al. 1995). These soils are very deep and well-drained from sandstone parent material. Mean annual temperature was estimated at 21–22°C with little intra-annual variation (Daly et al. 2003). Mean annual precipitation (1955–2005) was reported at approximately 2000 mm at 730 m above sea level at nearby Jajome Alto, Guayama (see Southeast Regional Climate Center web site).⁴

Our chronosequence included three replicate sites each of primary forests, and of secondary forests regrowing on pastures abandoned 10, 20, 30, 60, and 80 years ago. Ten of the forest sites were previously described in Pascarella et al. (2000, 2004) and correspond to their Carite, higher elevation sites. An additional eight sites and their land-use history were identified for our study using time-sequence aerial photographs (1936, 1951, 1967, 1977, 1988, and 1995) and interviews with local landowners. Wherever confirmation with landowners or neighbors was unavailable, time since pasture abandonment was estimated as the difference between the sampling year and the mid-point between the last photograph showing pasture use and the first photograph showing woody regrowth. Young secondary forests in the 1936 photos were at least 10 years old, the time taken for forest canopy to close in this region. Reforestation in this region occurred through natural regeneration. We use the term “primary” forest to refer to remnant forest fragments that have not been under pasture cover for at least the last century, if ever. These forest sites have not been actively

⁴(<http://www.sercc.com/climateinfo/historical/historical.html>)

TABLE 1. General and specific allometric equations used to calculate total aboveground biomass (TAB) in kg.

Forest type	Equation type	Author	Equation
Tabonuco	general, all dicots	Weaver and Gillespie (1992)†	TAB = 0.3210(dbh)exp(1.3925), for dbh = 0.3 to <5 cm TAB = 4.7306 – 2.8566(dbh) + 0.5832(dbh)exp(2), for dbh > 5 cm
Palm	species-specific	Lugo and Frangi (1985)‡	TAB = 9.7(ht) + 6.8

Note: Key to abbreviations: dbh, diameter (in cm) at breast height (1.3 m); ht, stem height.

† Generated for subtropical wet life zones in Puerto Rico.

‡ Generated for floodplain palm forest (*Prestoea acuminata* var. *montana*) at 750 m elevation in Puerto Rico.

managed, although local people occasionally collect palm fronds (E. Marín-Spiotta, *personal observation*), which is considered a non-intensive use.

Forest structure and composition

At each forest site, we established a 24 × 24 m plot to describe forest structure and species composition. All live, rooted trees with diameter at breast height (dbh) ≥ 10 cm and stem length of at least 1.3 m (hereafter called “large” trees) were tagged and identified to species according to Little and Wadsworth (1964) and Little et al. (1974). We counted all multiple stems from a single base that satisfied the dbh and height requirements. We calculated basal area, relative abundance and relative frequency for all stems with dbh ≥ 10 cm. Importance values were calculated as the sum of relative abundance and relative basal area for each species. At a subset of sites, in a 12 × 12 m area within the plot, we also measured and identified woody trees 1.5–10 cm dbh (hereafter called “small” trees) that were at least 1.3 m tall. Stem densities are reported for both size classes.

Biomass estimates

Total aboveground tree biomass (TAB) was estimated using previously published allometric equations (Table 1). We compared three general equations for dicotyledonous trees; two were derived from similar wet forest sites in Puerto Rico (Weaver and Gillespie 1992, Scatena et al. 1993), and one was a more general tropical equation developed for lowland wet tropical forest (Brown 1997). When tested on a subset of the data within comparable dbh size ranges (10–45.7 cm dbh), all three equations yielded similar results for aboveground biomass (data not shown). Divergences in biomass estimates for individual trees appeared for stems with dbh > 45.7 cm. An increase in the variation of estimates of individual large stem sizes has also been reported in other tropical studies (Keller et al. 2001, Brandeis and Suárez Roza 2005). However, because of the small number of trees with dbh > 45.7 cm, these differences were not reflected in total biomass estimates. For this reason, we report total biomass results using the Weaver and Gillespie (1992) equation, which covered the widest range of tree size classes measured at our sites, especially in the lower diameter sizes (<10 cm).

We also compared mean TAB estimates for several individual species (dbh ≥ 10 cm) where specific

equations were available to that calculated from the Weaver and Gillespie general equation to check for the appropriateness of using a general equation at these sites. Species- or genera-specific equations were available for *Casearia* spp., *Cecropia schreberiana*, *Schefflera morototoni* (Aubl.) Maguire et al., *Dacryodes excelsa* Vahl, *Inga* spp., *Ocotea* spp., *Ormosia krugii* Urban peronia, and *Sloanea berteriana* Choisy ex DC. (see Appendix 1 in Scatena et al. 1993). The Weaver and Gillespie equation approximated the species-specific equations in all but two cases: the Weaver and Gillespie equation gave significantly higher estimates of large tree biomass (in kilograms) for *Casearia* spp. ($\chi^2 = 76.3574$, $P < 0.0001$) and *Ocotea* spp. ($\chi^2 = 10.1471$, $P < 0.02$), relative to species-specific relationships.

We applied a specific allometric equation for the monocot palm, *Prestoea acuminata* var. *montana*, due to its abundance in the older forests. The equation used stem height rather than dbh (Frangi and Lugo 1985). The general equations, which were generated for dicotyledonous trees and used dbh as a biomass predictor, overestimated palm biomass by a factor of 2 or 3 compared to the palm-specific model (data not shown). TAB estimates did not include vines (which were not a significant component of these forests), tree ferns, or nonwoody understory species such as *Heliconia* spp. Carbon inventories in forests were calculated as 46% of TAB (our data). Total aboveground biomass of active pastures was estimated as 7.7 ± 1.5 Mg/ha (mean ± SE), which is an average of literature values for tropical pastures in similar life-zones and on similar soil types (Fearnside and Guimarães 1996, Wick et al. 2005), with C stocks calculated as 42% of plant biomass (our data).

Previous work has addressed uncertainties in biomass estimates, including those associated with small plot sizes, and error due to generalizing from allometric relationships (Brown et al. 1995, Chambers et al. 2001, Keller et al. 2001, Brandeis and Suárez Roza 2005). Small plot size increases the potential bias associated with spatially distributed factors such as tree fall gaps, rare species, and clonal species. The plot size used here was chosen based on the relatively small land holdings typical of recovering forests in the region. The allometric equation we used was developed using standing primary and secondary forests in Puerto Rico, which exist in relatively small patches. The lower diversity and

structural homogeneity of these montane forests, especially the young secondary forests, together with the fact that plots were spatially distinct and distributed over a relatively large area are likely to reduce variability in biomass estimates. Regardless, the data reported here are likely to be impacted by the plot size used and should not be extrapolated to larger plot sizes or regions where forest tracts cover a broader expanse.

Data analysis

Parametric and nonparametric analyses were performed on JMP version 5.1 software (SAS Institute 2004). All data were tested for normality and equal variance. If all requirements for normality were not met, we performed a nonparametric analysis (Wilcoxon/Kruskal-Wallis) to test for significant differences ($P < 0.05$) and then identified differences between groups by a Tukey-Kramer honestly significant difference (hsd) test. We used linear regressions to determine patterns with time since pasture abandonment in basal area, biomass, and carbon. For linear regressions over time, active pastures were set at 0 years and primary forests were not included since we are uncertain of their actual age. We performed a nonmetric multidimensional (NMS) scaling analysis with 400 iterations on the importance values of the large tree data set across the different sites (PC-ORD V. 4; MjM Software Design, Gleneden Beach, Oregon, USA).

RESULTS

Species composition

We measured 892 stems with dbh ≥ 10 cm and 1423 stems in the 1.5 to <10 cm dbh size class. We encountered at least 56 species from 38 genera and 26 families (Tables 2 and 3). The most important species was *Tabebuia heterophylla*, with 265 stems and a basal area of 108 m²/ha (Table 4). The distribution of the 12 most important species changed across the chronosequence (Fig. 1). *T. heterophylla* was the dominant large tree in the first 30 years after reforestation and was absent from the primary forests. The second most important species was the palm *P. acuminata* var. *montana*, which dominated the older secondary forest sites (60, 80 years) and primary forests. The third most abundant species, *Syzygium jambos* (L.) Alston, was present at all ages except for the 30-year-old sites. The nitrogen-fixer, *Inga laurina* Willd., in the family Fabaceae, and the common pioneer species, *C. schreberiana* and *S. morototoni*, were among the top seven in terms of basal area and abundance (Table 4). Of the top 12 most important species across our sites, all except for *S. jambos* were native to Puerto Rico. The following endemic species had individuals in the large tree size classes of secondary forests: *Sapium laurocerasus* Desf. and *Eugenia stahlii* (Kiaersk.) Krug and Urban, and in the understory of successional forests: *Cordia borinquensis* Urban and *Hirtella rugosa* Thuill ex Pers.

The NMS analysis on importance values of large tree species separated sites into three main groups: the younger secondary forests (10, 20, and 30), the older secondary forests (60 and 80) and the primary forests (Fig. 2). The final stress for a two-dimensional analysis was 0.114. The primary forests had a distinct species composition. *Dacryodes excelsa*, the dominant primary forest species of low to mid elevation forests in the region, was exclusively found in the primary forest sites, where it accounted for up to 30% of all large stems and an average 24% of total basal area. Seven other species, including two endemic to Puerto Rico, were also found only in the primary forests (Table 2). Species richness, measured as the total number of species in the ≥ 10 cm dbh size class per plot, differed by forest age. The younger secondary forests (10, 20, and 30 years) averaged lower number of species than the older forests (60 years, 80 years, and primary) ($F_{1,16} = 16.9162$, $P = 0.0008$; Table 5). Primary forests did not differ in species richness from the older secondary forests.

One of the 20-year-old forests had three stems with dbh > 34.9 cm and one stem, an *Inga vera*, was recorded at 68.2 cm in diameter. Large remnant pasture trees are rare in these sites, so it is more likely that this site had a secondary, agricultural land use. This site also had a number of fruit trees (*Citrus* spp. and *Mangifera indica* L.), which were actively harvested by the current land owners. It was the only secondary forest site without any *T. heterophylla* and contained the only specimen we encountered of the nonnative African tulip tree, *Spathodea campanulata* Beauv. *S. campanulata* was common along the major roads in the region, although our sites were far from the main roadways. Excluding this site from the analysis had no effect on the results so we included it here.

Forest structure

The 10-year-old sites were the only ones that differed in stem density along the chronosequence, and they had significantly higher small stem density and significantly lower large stem density than all other forest sites ($P < 0.01$; Table 5). The distribution of stems by diameter size class showed the largest number of stems in the smaller size classes (Fig. 3). The contribution of larger size classes increased with time (Fig. 4). Trees > 25 cm in diameter did not appear until 20 years of secondary growth. Their contribution to total forest structure steadily increased from the 20- to 60- to 80-year-old secondary forests. The number of stems with diameter > 35 cm also increased with forest age. The 80-year-old secondary forests had the highest proportion of large stems in the 25–34.9 cm size class, and the greatest number of stems > 50 cm.

Basal area

Over 80 years of succession, time since pasture abandonment explained 77% of the variability in basal area of trees with dbh ≥ 10 cm in the secondary forests

TABLE 2. Mean relative abundance of trees with dbh \geq 10 cm.

Species	Family	Plant type	Age of secondary forests derived from pasture (yr)					Primary forests	
			10	20	30	60	80		
<i>Alchornea latifolia</i>	Euphorbiaceae	N		0.04			0.10	0.05	0.04
<i>Andira inermis</i>	Fabaceae	N						0.02	
<i>Buchenavia capitata</i>	Combretaceae	N					0.02	0.03	0.02
<i>Casearia arborea</i>	Flacourtiaceae	N			0.08		0.11	0.06	0.11
<i>Casearia sylvestris</i>	Flacourtiaceae	N			0.01				
<i>Cassipourea guianensis</i>	Rhizophoraceae	N		0.07					
<i>Cecropia schreberiana</i>	Moraceae	N		0.22			0.03	0.05	0.04
<i>Chrysophyllum argenteum</i>	Sapotaceae	N							0.02
<i>Citiharexylum fruticosum</i>	Verbenaceae	N		0.05					
<i>Citrus paradisi</i>	Rutaceae	L					0.03		
<i>Citrus</i> spp. (others)	Rutaceae	L		0.09					
<i>Clusia</i> spp.	Clusiaceae	N			0.02				
<i>Coccoloba diversifolia</i>	Polygonaceae	N							0.02
<i>Cordia alliodora</i>	Boraginaceae	N					0.03		
<i>Cordia borinquensis</i>	Boraginaceae	EN							0.02
<i>Cordia collococca</i>	Boraginaceae	N							0.02
<i>Cordia sulcata</i>	Boraginaceae	N						0.02	
<i>Cordia</i> spp. (others)	Boraginaceae	N						0.03	0.02
<i>Cyathea arborea</i>	Cyatheaceae	N	0.23	0.11	0.02			0.02	
<i>Dacryodes excelsa</i>	Burseraceae	N							0.17
<i>Eugenia stahlii</i>	Myrtaceae	EN						0.07	
<i>Ficus laevigata</i>	Moraceae	N					0.01		
<i>Ficus</i> spp.	Moraceae	N						0.02	
<i>Guarea guidonia</i>	Meliaceae	N		0.02	0.02				
<i>Hirtella rugosa</i>	Rosaceae	EN							0.02
<i>Homalium racemosum</i>	Flacourtiaceae	N					0.07	0.04	0.08
<i>Inga laurina</i>	Fabaceae	N	0.50		0.02		0.10	0.07	0.02
<i>Inga vera</i>	Fabaceae	N		0.07					
<i>Mangifera indica</i>	Anacardiaceae	L		0.02					
<i>Meliosma herbertii</i>	Sabiaceae	N							0.02
<i>Miconia tetrandia</i>	Melastomataceae	N							0.02
<i>Miconia</i> spp. (others)	Melastomataceae	N	0.08					0.03	
<i>Micropholis chrysopholloides</i>	Sapotaceae	N						0.07	0.09
<i>Myrcia deflexa</i>	Myrtaceae	N					0.02		
<i>Myrcia leptoclada</i>	Myrtaceae	N						0.02	0.02
<i>Myrcia splendens</i>	Myrtaceae	N			0.02		0.05	0.03	
<i>Myrcia</i> spp. (others)	Myrtaceae	N			0.06			0.03	
<i>Ocotea floribunda</i>	Lauraceae	N						0.02	
<i>Ocotea leucoxydon</i>	Lauraceae	N		0.04	0.02		0.14	0.04	0.02
<i>Ormosia krugii</i>	Fabaceae	N					0.01		
<i>Prestoea acuminata</i>	Arecaceae	N		0.02			0.21	0.22	0.50
<i>Sapium laurocerasus</i>	Euphorbiaceae	EN					0.02		
<i>Schefflera morototoni</i>	Araliaceae	N	0.08	0.07	0.06		0.10	0.06	0.02
<i>Sloanea berteriana</i>	Elaeocarpaceae	N						0.13	0.02
<i>Spathodea campanulata</i>	Bignoniaceae	L		0.02					
<i>Syzygium jambos</i>	Myrtaceae	L	0.25	0.15			0.27	0.10	0.04
<i>Tabebuia heterophylla</i>	Bignoniaceae	N	0.54	0.72	0.85		0.05	0.08	
<i>Turpinia paniculata</i>	Staphyleaceae	N					0.05		
<i>Vitex divaricata</i>	Verbenaceae	N							0.05

Note: Abbreviations: N, native; EN, endemic; L, naturalized.

(one-way ANOVA, $P < 0.0001$, $F_{1,13} = 43.49$). Basal area of large trees ranged from 0.1 m²/ha in a 10-year-old forest site to 54.5 m²/ha in an 80-year-old secondary forest site (Table 5). Average basal area in the primary forest sites was 28.9 m²/ha, which was significantly lower (Tukey-Kramer hsd all means comparisons, $P < 0.05$) than average basal area for the oldest secondary forest sites (46.9 m²/ha, 80 years old), but similar to the 20-, 30-, and 60-year-old secondary forests. In the 10-year-old sites, trees with dbh $<$ 10 cm contributed an average of 20 times as much as large trees to total basal area (Table 5). The oldest secondary forests (80 years), which

had the highest average basal area of large trees, also had the lowest basal area of small trees.

Biomass estimates and C accumulation rates

The 80-year-old forests had approximately 272 Mg/ha of aboveground biomass (125 Mg C/ha) in stems \geq 1.5 cm dbh (Table 6). Time since pasture abandonment explained 72% of the variability in TAB (all trees dbh \geq 1.5 cm; one-way ANOVA, $F_{1,12} = 31.5060$, $P = 0.0001$). The 80-year-old secondary forests had significantly greater biomass in the \geq 10 cm tree size classes (269 ± 49 Mg/ha) than the primary forests (161 ± 16 Mg/ha). Large tree biomass accumulated at an average rate of 2.9

TABLE 3. Species and plant types in the smaller diameter size classes (<10 cm and >1.5 cm).

Species	Family	Plant type
<i>Alchornea latifolia</i>	Euphorbiaceae	N
<i>Casearia arborea</i>	Flacourtiaceae	N
<i>Casearia sylvestris</i>	Flacourtiaceae	N
<i>Cecropia schreberiana</i>	Moraceae	N
<i>Cestrum macrophyllum</i>	Solanaceae	N
<i>Citharexylum fruticosum</i>	Verbenaceae	N
<i>Cordia borinquensis</i>	Boraginaceae	EN
<i>Cyathea arborea</i>	Cyatheaaceae	N
<i>Daphnopsos americana</i>	Thymelaeaceae	N
<i>Hirtella rugosa</i>	Rosaceae	EN
<i>Miconia prasina</i>	Melastomataceae	N
<i>Miconia</i> spp. (others)	Melastomataceae	N
<i>Miconia tetrandia</i>	Melastomataceae	N
<i>Myrcia deflexa</i>	Myrtaceae	N
<i>Myrcia splendens</i>	Myrtaceae	N
<i>Ocotea leucoxyton</i>	Lauraceae	N
<i>Prestoea acuminata</i> var. <i>montana</i>	Arecaceae	N
<i>Psidium guajava</i>	Myrtaceae	L
<i>Psychotria berteriana</i>	Rubiaceae	N
<i>Psychotria brachiata</i>	Rubiaceae	N
<i>Schefflera morototoni</i>	Araliaceae	N
<i>Syzygium jambos</i>	Myrtaceae	L
<i>Tabebuia heterophylla</i>	Bignoniaceae	N
<i>Turpinia occidentalis</i>	Staphyleaceae	N

Note: Abbreviations: N, native; EN, endemic; L, naturalized.

± 0.4 Mg·ha⁻¹·yr⁻¹ over the chronosequence. The fastest increase in biomass occurred in the first 20 years since pasture abandonment, at an average rate of 6.3 ± 1.1 Mg·ha⁻¹·yr⁻¹. Further accumulation of biomass occurred between 30 and 60 years of reforestation, though at a slower rate: 2.6 ± 0.5 Mg·ha⁻¹·yr⁻¹. Standing live aboveground biomass accumulated C over the successional sequence at an average rate of 1.3 ± 0.2 Mg C·ha⁻¹·yr⁻¹.

DISCUSSION

Changes in forest community composition and structure

Secondary forests recovered many structural characteristics of primary forests in the first two decades since forest re-establishment on abandoned pastures. The 10-year-old forests had more small stems and fewer large

TABLE 4. Total number of stems and basal area of the top 12 most important species in the ≥10 cm dbh size class.

Genus and species name	Total no. stems	Total basal area (m ² /ha)
<i>Tabebuia heterophylla</i>	265	108.4
<i>Prestoea acuminata</i> var. <i>montana</i>	166	67.4
<i>Syzygium jambos</i>	47	19.5
<i>Casearia arborea</i>	42	10.9
<i>Cecropia peltata</i>	39	28.5
<i>Inga laurina</i>	38	21.8
<i>Schefflera morototoni</i>	37	23.8
<i>Ocotea leucoxyton</i>	27	9.4
<i>Alchornea latifolia</i>	23	12.2
<i>Dacryodes excelsa</i>	18	13.7
<i>Cyathea arborea</i>	18	4.0
<i>Sloanea berteriana</i>	12	24.5

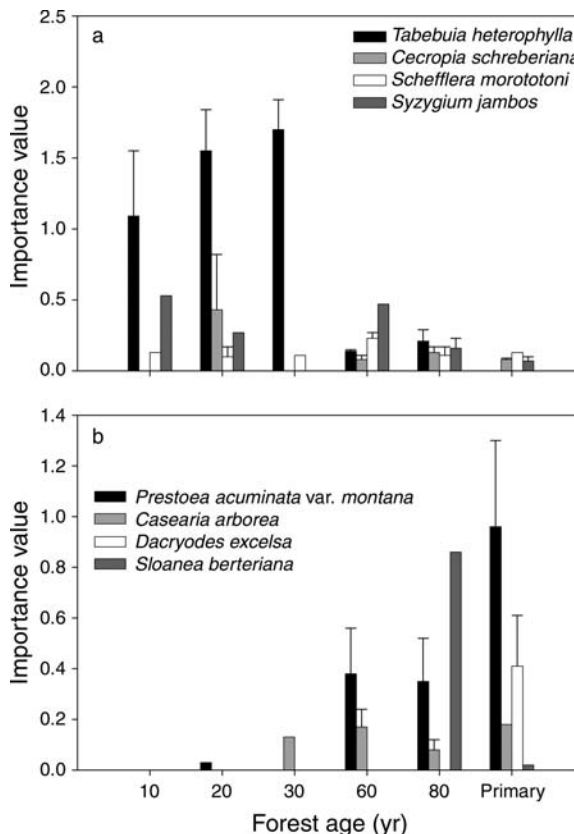


FIG. 1. Importance values (mean + SE) of selected tree species out of the top 12 most important in the ≥10 cm dbh size class in primary forests and secondary forests regrowing on abandoned pastures. (a) Most important pioneer species and (b) mature forest species across a chronosequence in the wet subtropical forest life zone of southeastern Puerto Rico.

trees than any of the other forest sites, but from 20 years of regrowth onward there were no significant differences in stem densities between secondary and primary forest sites. Basal area of 20-year-old secondary forest sites was also similar to that of the primary forests. Species composition, however, remained distinct even after 80 years of secondary succession. Large tree species composition separated the sites by successional stage and land use history. Early successional forests (10, 20, and 30 years old) were distinguished from the later successional stages (60- and 80-year-old forests). The early successional forests were heavily dominated by *T. heterophylla*, a common colonizer of abandoned pastures (Aide et al. 1996, China and Helmer 2003). *T. heterophylla* was present in the older secondary forests, but lost dominance over succession as other species increased in importance. A number of stems of *T. heterophylla*, which is commonly used as a live fence, exhibited barbed wire scars. Though dominant in secondary forests, this species was absent from the primary forests, supporting our historical interpretation that these sites were never under pasture use.

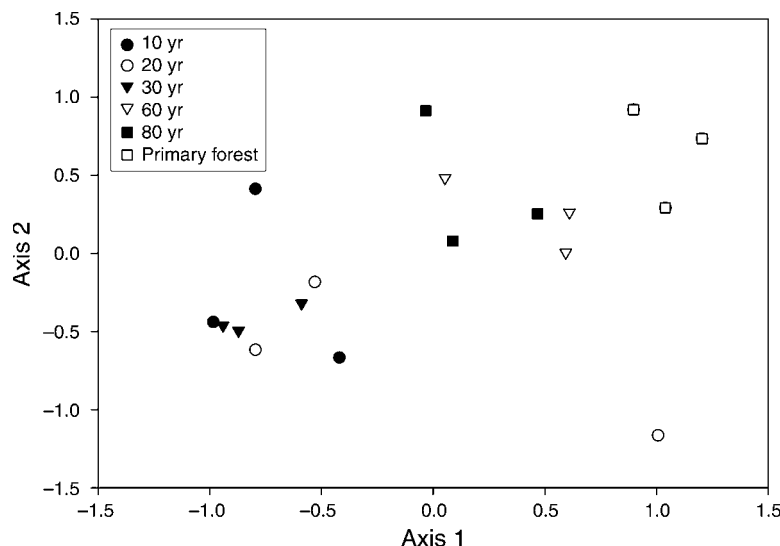


FIG. 2. Nonmetric multidimensional scaling (NMS) ordination results for importance values of all tree species represented in the ≥ 10 cm dbh size class in primary and secondary forests regrowing on abandoned pastures in the wet subtropical life zone of southeastern Puerto Rico.

Species composition may explain differences in forest structure, particularly stem density and basal area or biomass, across sites. In the youngest secondary forests, the high density of stems was due to the presence of many multitemmed individuals, especially of *Miconia* spp. and *S. jambos*. This regeneration of multiple stems, or coppicing, is typically a result of clearing by hand and has been reported for other young secondary forests (Aide et al. 1995, 2000). Slightly more than half (56%) of individual trees in the 10-year-old secondary forests had two or more stems. The maximum number of stems recorded for one individual was 27 (a *Miconia* spp.). *S. jambos* and *Miconia* spp. are often the first woody invaders on abandoned pastures in Puerto Rico (Aide et

al. 1996, Myster 2003), replacing the typical pioneer species (e.g., *C. schreberiana*, *S. morototoni*), though these do appear later in secondary succession (Aide et al. 1995; this study).

The 30-year-old sites showed differences from the younger and older secondary forests that may reflect a successional change, mainly through a reorganization in structure and composition. The 30-year-old sites exhibited less stem size differentiation than the 20-year and older secondary forests. The 30-year-old sites were also heavily dominated by *T. heterophylla*, with an average importance value of 1.7 out of a possible maximum of 2. The homogeneous stem distribution may be explained by most of the stems belonging to the same cohort with

TABLE 5. Mean (SE) stem density for large and small trees.

Age	No. sites	Species richness	Stem density (no. stems/ha)	Basal area (m ² /ha)
dbh ≥ 10 cm				
Secondary forests				
10 yr	3	3.0 ^a (1.2)	104 ^a (63)	1.4 ^a (1.0)
20 yr	3	8.3 ^{ab} (3.5)	845 ^b (93)	23.7 ^b (3.5)
30 yr	3	5.7 ^{ab} (2.7)	1048 ^b (113)	16.9 ^{ab} (1.2)
60 yr	3	13.7 ^{bc} (1.5)	1076 ^b (44)	32.5 ^{bc} (1.9)
80 yr	3	19.3 ^c (4.2)	1163 ^b (36)	46.9 ^c (7.1)
Primary forests	3	13.7 ^{bc} (3.4)	926 ^b (95)	28.9 ^b (1.5)
1.5 cm < dbh < 10 cm				
Secondary forests				
10 yr	2	n.m.	30 729 ^a (2396)	21.2 ^a (1.3)
30 yr	1	n.m.	5139 ^b	7.2 ^{ab}
60 yr	2	n.m.	6771 ^b (1076)	8.1 ^b (1.7)
80 yr	2	n.m.	1806 ^b (694)	2.6 ^b (1.3)
Primary forests	3	n.m.	3889 ^b (1776)	5.0 ^b (2.2)

Notes: Different letters following values represent significant differences at $P < 0.05$ within columns; n.m., not measured.

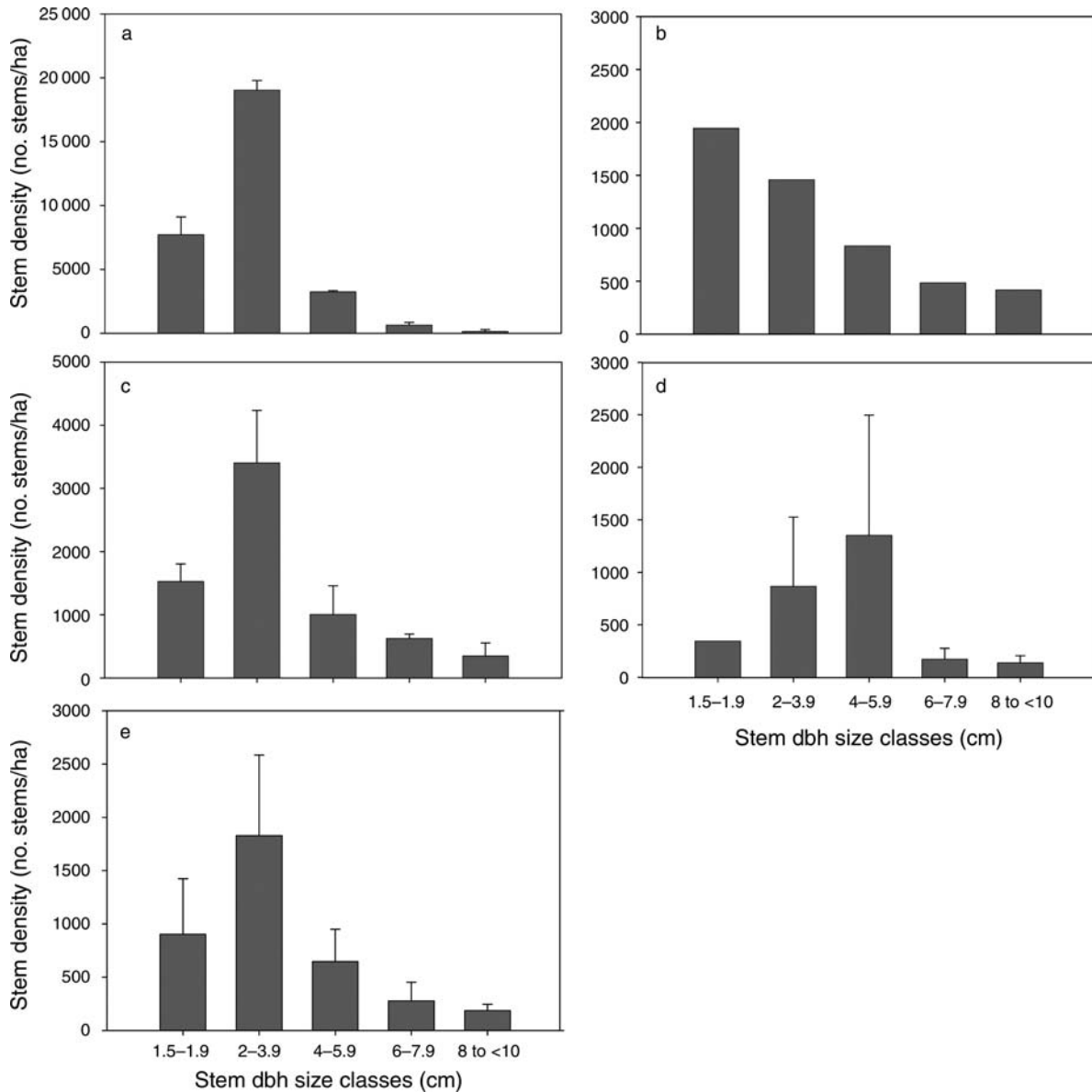


FIG. 3. Distribution of small-diameter stems (<10 cm dbh) in (a) 10-year-old secondary forest, (b) 30-year-old secondary forest, (c) 60-year-old secondary forest, (d) 80-year-old secondary forest, and (e) primary forest in the wet subtropical life zone of southeastern Puerto Rico. Values are means + SE.

similar growth rates. A notable difference between the 30-year-old sites and all other secondary forest sites is the absence of the naturalized rose-apple, *S. jambos* from the dbh ≥ 10 cm size class. *S. jambos* is typically a very common post-disturbance invader (Brown et al. 2006), present as a large tree in all later stages of our chronosequence, though in the 10- and 20-year-old sites there were only two individuals. The 60-year-old forests, on the other hand, had several large individuals of *S. jambos*, and the 80-year-old secondary forests had twice as many. This suggests that *T. heterophylla* is more important as a colonizer during the early stages of succession, and after 30 years, *S. jambos* becomes more

important. Alternatively, it is possible that the differences between the 30-year-old sites and other successional forests reflect a difference in previous land use management or seed source for reforestation, which are impossible to determine at this point in time. The fact that all three replicates of the 30-year-old sites showed the same pattern, and that they were spatially distinct and distributed over a large area gives more credence to our first hypothesis.

The oldest successional forests differed from the primary forests, not only in terms of species composition, but also in structure. The 80-year-old sites had the highest average total basal area, lowest average total

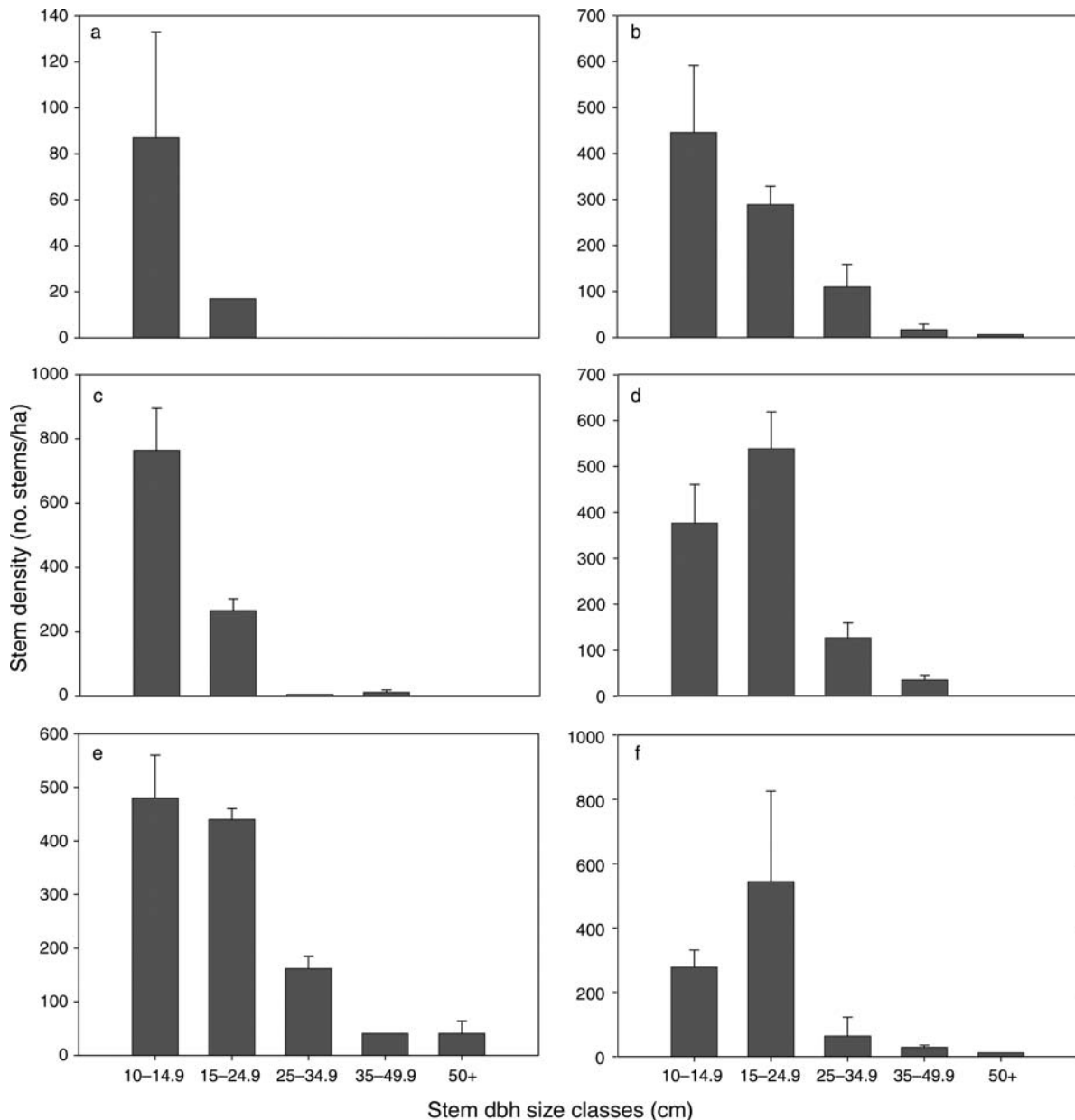


FIG. 4. Distribution of large-diameter stems (≥ 10 cm dbh) in (a) 10-year-old secondary forest, (b) 20-year-old secondary forest, (c) 30-year-old secondary forest, (d) 60-year-old secondary forest, (e) 80-year-old secondary forest, and (f) primary forest in the wet subtropical life zone of southeastern Puerto Rico. Values are means + SE.

stem density, and contained the highest proportion of trees with diameters > 25 cm. Biomass estimates of 80-year-old secondary forests were, on average, significantly higher than primary forests. Species composition may explain these structural differences, mainly the distribution of palms vs. dicot woody species. Palm biomass was lower than that of dicot species with comparable stem sizes. The dominant species in the primary forests was *Prestoea acuminata* var. *montana*, with an average importance value of 0.96 compared to 0.35 in the 80-year-old forests. Palms are monocots, which do not

exhibit lateral woody growth with age, and all but one palm fell in the diameter range of 10.4 to 35 cm. In the 80-year-old secondary forests, all trees with dbh > 50 cm ($n = 7$) were dicot woody species, accounting for approximately 120 Mg of additional aboveground biomass relative to the primary forests.

Land-use history can have long-term implications for the forest community composition and diversity, and it is unknown whether the original species composition will ever be restored (Lugo and Helmer 2004). While many of the primary forest species were not present in

the canopy of the secondary forest sites, we found at least two of the primary forest species, which are also endemic to Puerto Rico, *Cordia borinquensis* and *Hirtella rugosa*, in the understory of the successional forests. Further work would need to be done to establish whether the emergence of these species in successional forests is due to their survival in the soil seed bank even under different land cover, or to propagation from external seed sources. Their presence, however, suggests that secondary forests recovering from agricultural disturbance can be important for maintaining species diversity, even if species composition is not the same as primary forests (Aide et al. 2000). In contrast with other secondary forests across Puerto Rico, which are dominated by nonnative species, notably the naturalized *Spathodea campanulata* (Rivera and Aide 1998, Pascarella et al. 2000, Lugo and Helmer 2004), all but one of the top 12 most important species at our sites were native.

Aboveground biomass and carbon sequestration

Secondary forests in this region recovered aboveground biomass values of primary forests within 20 years after pasture abandonment. This was in sharp contrast with other studies, which have found much longer times for recovery of biomass of mature, undisturbed forests. For example, Saldarriaga et al. (1988) estimated that it would take 189 years for tropical moist tierra firme forests in Venezuela recovering from slash and burn agriculture to recover aboveground biomass. Aboveground biomass accumulation rates are typically faster in the first two decades of tropical forest regeneration on abandoned agricultural and pasture lands (Silver et al. 2000). The recovering forests in this study accumulated biomass at rates very similar to the average of $6.2 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ from a review of the tropical literature on the first 20 years of succession (Silver et al. 2000), but lower than those for lowland tropical terra firme forests ($10 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in 8 years [Uhl et al. 1988] and $11 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in 14 years [Feldpausch et al. 2004]). Over 80 years of reforestation, our biomass accumulation rates were remarkably similar to the global average rate for tropical secondary forests of $2.9 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Silver et al. 2000).

Rates of C accumulation over 60 years ($1.2 \pm 0.2 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ [mean \pm SE]), were similar to rates reported in secondary forests of comparable age in the subtropical moist life zone of Puerto Rico ($1.4 \pm 0.05 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; Silver et al. 2004). The similarity of these rates is remarkable, given that the secondary forest site in the Silver et al. (2004) study had been actively replanted, while our chronosequences were examples of natural regeneration.

Conclusions

The secondary forests in this study achieved several of the structural characteristics of primary forests within 20 years of pasture abandonment, but the plant community

TABLE 6. Total aboveground biomass (TAB) estimates from the Weaver and Gillespie (1992) general allometric biomass equation for large trees (dbh ≥ 10 cm) and all trees (dbh ≥ 1.5 cm) across a secondary forest chronosequence in Puerto Rico.

Age	TAB for trees ≥ 10 cm dbh (Mg/ha)	TAB for trees ≥ 1.5 cm dbh (Mg/ha)
Secondary forests		
10 yr	6 ^a (5)	53 ^a (6)
20 yr	135 ^b (25)	135 ^{ab} (25)
30 yr	89 ^{ab} (5)	97 ^{ab} (10)
60 yr	166 ^b (4)	181 ^{bc} (7)
80 yr	269 ^c (41)	272 ^c (43)
Primary forests		
	161 ^b (16)	173 ^{abc} (19)

Notes: Values are means with SE in parentheses. Different letters following values represent significant differences at $P < 0.05$ within columns.

remained distinct from primary forests even after eight decades of secondary succession. Successional stage affected species composition, with early stages of reforestation (10, 20, and 30 years) differing from later stages of succession (60 and 80 years). Changes in the plant community during secondary succession were responsible for the biomass differences between secondary and primary forests. The 80-year-old secondary forests had more dicot woody species, and greater aboveground biomass, than primary forests, which were dominated by palms. Though species composition in secondary forests differed from forests that had not been under pasture use, some of the primary forest species and species endemic to Puerto Rico were present in the understory of secondary forests. These new secondary forests may provide an opportunity for the conservation of biodiversity in a human influenced landscape. In this study, secondary forests sequestered an average of 130 Mg C/ha in aboveground biomass in the last 80 years. The long-term potential of these secondary forests to sequester C and fulfill forest ecosystem services depends on their future fate. Urbanization is currently encroaching upon secondary forests across the island (Thomlinson and Rivera 2000, Helmer 2004). The past trend in natural reforestation in Puerto Rico (Grau et al. 2004) may be reversed as secondary forests are re-cleared, this time for commercial and residential development, rather than for agriculture.

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