Caribbean Journal of Science, Vol. 41, No. 2, 250-268, 2005

Effects of Model Choice and Forest Structure on Inventory-Based Estimations of Puerto Rican Forest Biomass

THOMAS J. BRANDEIS[1] AND MARÍA DEL ROCÍO SUÁREZ ROZO[2]

[1] *USDA Forest Service, Southern Research Station, Forest Inventory and Analysis, 4700 Kingston Pike, Knoxville, TN 37919;*
[2] *University of Puerto Rico at Mayagüez, College of Agricultural Sciences Department of Agricultural and Biosystems Engineering P.O. Box 9030, Mayagüez, PR 00681-9030*
Corresponding author: tjbrandeis@fs.fed.us

ABSTRACT.—Total aboveground live tree biomass in Puerto Rican lower montane wet, subtropical wet, subtropical moist and subtropical dry forests was estimated using data from two forest inventories and published regression equations. Multiple potentially-applicable published biomass models existed for some forested life zones, and their estimates tended to diverge with increasing tree diameter at breast height. Inventoried forests showed structural characteristics typical of secondary tropical forests and stand successional trends of increasing stem density from initial reversion to young closed forest, followed by a decrease in stem density and gradual increase in basal area and biomass as the stands developed. Stems with D_{BH} < 10 cm contributed 9.9-50.9% of total aboveground biomass. When present, 50-90+ cm D_{BH} trees greatly increased aboveground biomass values on individual plots, but these effects subsided when averaged over the forested landscape. Inherent variability in large-tree form combined with equations that extrapolate beyond the range of sampled trees impedes accurate aboveground biomass estimation for larger trees. Application of equations developed in areas that most closely match potential study sites should improve overall estimation accuracy of all forest stands, however, locally developed biomass equations are lacking for subtropical dry and perhaps subtropical moist forest life zones in Puerto Rico.

KEYWORDS.—Biomass, forest inventory, Puerto Rico, Río Grande de Arecibo

INTRODUCTION

Following extensive deforestation (Wadsworth 1950), Puerto Rico's secondary forests developed into a unique combination of native Caribbean tree species and tree species introduced from tropical areas around the world (Lugo and Helmer 2004). Assessing the health and function of these new forest ecosystems requires a long-term inventory and monitoring effort. Estimating carbon fixed by and stored in tropical forest ecosystems provides insight into local and global biogeochemical cycles (Brown and Lugo 1982; Brown and Lugo 1990; Dixon et al. 1994; Grau et al. 2004; Phillips et al. 1998), so while past forest inventories in Puerto Rico focused on wood volume and tree basal area (Birdsey and Weaver 1982; Franco et al. 1997), current inventories require accurate assessments of biomass and carbon. However, studies in other tropical forests have shown that uncertain biomass estimates complicate the quantification of forest carbon storage and fluxes (Brown et al. 1995; Houghton et al. 2000; Houghton et al. 2001; Nascimento and Laurance 2002). Regression equations used to estimate individual tree biomass have been cited as a source of significant error, particularly for larger trees (Overman et al. 1994; Clark and Clark 2000; Keller et al. 2001; Chave et al. 2004).

Derivation of regression equations through destructive sampling allows researchers to model live tree aboveground biomass (AGB) as a function of one or more standing tree dimensions such as tree stem diameter at breast height (D_{BH} at 1.37 m) and tree height (H_t) (Parresol 1999). Large-

---

ms. received October 28, 2004; accepted May 22, 2005.

scale biomass estimates can be made for forested areas by applying these equations to individual trees in the forest inventory sample (Birdsey 1992; Brown 1997; Smith et al. 2004). Ideally, regression equations that estimate AGB would be available for each individual tree species over its entire range of potential sizes and growth forms. Work done in temperate forests approaches but still has not reached this ideal (See Cost and McClure 1982 for an example). In any case, this approach is not currently practical for diverse tropical forests, such as those of Puerto Rico where an island-wide forest survey might encounter up to 659 tree species (Little et al. 1974; Francis and Liogier 1991). Creating regression equations for species groupings rather than individual species (Whittaker and Marks 1975; Nelson et al. 1999; Brown 2002), or individual equations for only the dominant species (Scatena et al. 1993; Nelson et al. 1999) are accepted compromise solutions that most of the forestry and forest ecology studies in tropical forests use, including those in Puerto Rico. A representative sample of trees from within a geographic area, life zone, forest type, or combination of these factors, is used to develop a single regression equation. Applying this approach more broadly, Brown et al. (1989) and Brown (1997) presented different models for estimating tropical forest biomass globally using tropical forest data sets from several countries.

Research in Puerto Rico has provided locally-developed regression equations that estimate AGB in oven-dry kilograms by using individual tree diameter at 1.37 m (D_{BH}) and total height (H_t) measurements. For some forest types, more than one equation is potentially available for estimating AGB. Equations are generally grouped according to Holdridge life zone, specifically subtropical lower montane rain, subtropical lower montane wet, subtropical wet, subtropical moist, and subtropical dry forest (Ewel and Whitmore 1973).

The objectives of this study are to (1) review the literature for AGB regression equations applicable to the subtropical lower montane rain/wet, subtropical wet, subtropical moist and subtropical dry forested life zones in Puerto Rico, (2) describe the structure of the inventoried forests in terms of stem density and basal area, and provide individual tree and per hectare AGB estimates calculated by applying existing models to data from two forest inventories, by life zone and soil parent materials, (3) compare estimates made for life zones with multiple available AGB equations, (4) assess AGB at different forest successional stages, and (5) evaluate the influence of small (D_{BH} < 10cm) and large (D_{BH} > 50-90cm) tree density and distribution on final average AGB estimates.

MATERIALS AND METHODS

Forest inventory data sets

Data from two Puerto Rican forest inventories were used to make AGB estimates; the island-wide USDA Forest Service, Forest Inventory and Analysis (FIA) forest survey, and the University of Puerto Rico's "NASA.—University Research Center, Tropical Center for Earth and Space Studies, Atmospheric Carbon Sequestration in Tropical Watersheds" survey of the of the upper reaches of the watershed of the Río Grande de Arecibo (RGA).

The island-wide FIA forest inventory of 2001-2003 used a systematic sample (for details on the inventory design see Brandeis 2003) which sampled all forest types and ownership categories across the 890,000 ha island, thus avoiding plot selection bias (Brown and Lugo 1992; Houghton et al. 2001; Phillips et al. 2002). Forest was defined using the FIA program definitions: at least 10% tree canopy coverage and a minimum area of 0.4 ha, or be at least 37 m wide if a strip. The sample unit consisted of a cluster of four subplots each with a 7.3 m radius. All trees with $D_{BH} \geq 12.5$ cm within the subplots were measured. All saplings with $D_{BH} \geq 2.5$ cm were measured within 2.1 m radius microplots nested within each subplot. For buttressed trees, D_{BH} was taken above the buttress and measurement height noted. All stems with $D_{BH} \geq 2.5$ cm were included in the AGB estimates even though not all the equations used for estimating biomass in this study were developed from data that included sapling-sized trees.

Crews located FIA plots with GPS units. A Geographic Information System (GIS) was used to assign Holdridge ecological life zones and parent material stratum from plot geographic coordinates. The FIA data set used in this study consists of 7 plots in the lower montane rain/wet forest with 315 trees, 72 plots in subtropical wet forest with 2,128 trees, 136 plots in subtropical moist forest with 3,640 trees, and 24 plots in the subtropical dry forest with 532 trees, for a total of 6,615 trees. An additional 38 plots categorized as recent reversions back to forest (< 10% forest tree canopy coverage) with 312 trees were separated from the main analyses because the goal was to first quantify AGB in more developed forests. Reversion plots were used in a separate analysis examining AGB changes over the course of stand development.

The second data set comes from a forest inventory of the upper reaches of the Río Grande de Arecibo watershed (RGA). After subtracting non-sampled areas such as water bodies, landslides, alluvial deposits, agriculture and urban/developed area, RGA has an area of 27,300 ha. It was inventoried in the summer 2003 by students of the University of Puerto Rico, Recinto Mayagüez using a stratified random design. Details on the inventory design are available in Suárez-Rozo (2004). The number of plots was proportional to the area of each stratum and the number of days available to carry out field work. A total of 4,469 trees with $D_{BH} \geq 10.0$ cm were measured in 91, 0.1 ha square plots that were stratified by Holdridge ecological life zone and geological parent material. Total area for each forest type and parent material stratum was derived from 2001 Landsat imagery and GIS coverages (Suárez-Rozo 2004). The RGA inventory data used for this analysis gave 4 plots in lower montane wet forest with 234 trees, 47 plots in subtropical wet forest with 2,119 trees, and 8 plots in subtropical moist forest with 427 trees.

Although standing dead trees were tallied in both inventories, only live trees were included in the AGB estimates. Shrubs and woody vines were not included in either inventory, so their biomass is not included in the estimates of AGB. Mangroves and other forest types of lesser extent that occur on Puerto Rico were not addressed by this study because the data sets used did not provide a sufficient number of samples.

Biomass models

We estimated individual tree AGB in kilograms (oven dry weight) for both data sets by applying the published regression equations by life zone (Table 1). All models estimate individual tree total AGB (woody plus foliage biomass). When authors provided more than one model, the models that used both D_{BH} and H_t tree measurements were chosen over those models that used D_{BH} alone because height potentially improves estimation precision (Brown 2002). Details on each life zone's models follow.

Lower montane rain/wet forest equations.—Species typical of the palo colorado forest type (*Cyrilla racemiflora* L., *Ocotea spathulata* Mez., *Micropholis chrysophylloides* Pierre and *Micropholis garciniaefolia* Pierre), elfin forest type (*Eugenia borinquensis* Britton, *Tabebuia rigida* Urban, *Weinmannia pinnata* L. and *Calycogonium squamulosum* Cogn.) and the palm brake forest type (dominated by *Prestoea montana* (Graham) Nichols.) are found in the lower montane forest life zones of Puerto Rico (Ewel and Whitmore 1973). Weaver and Gillespie (1992) developed regression equations for determining total aboveground woody biomass and total AGB (woody plus foliage biomass) in oven-dry kg/tree using D_{BH} and $D_{BH}{}^2H_t$ as the predictors for the lower montane rain and wet forest (elfin and palo colorado forest types) in the Caribbean National Forest. Trees in their data set ranged from 0.3-45.7 cm in diameter, and 1.3-20.7 meters in height. Fifty-six trees with $D_{BH} < 5$ cm and 29 trees with $D_{BH} \geq 5$ cm from 45 species were destructively sampled.

The equation that estimated total biomass from $D_{BH}{}^2H_t$ for elfin forest was used for lower montane rain forest, and the similar equation for palo colorado forest was used for lower montane wet forest (Table 1). However, there was only one plot in both

TABLE 1. Regression equations used, by life zone. (Y_T = weight, total (oven-dry kg/tree including stem, branches and foliage), D_{BH} = Diameter (cm) at 1.37 m, H_t = total height (m), BA = basal area (m^2))

Subtropical lower montane rain forest		
$Y_T = 0.1338 *(D_{BH}^{0.6487})$		(Weaver and Gillespie 1992)
Subtropical lower montane wet forest		
$Y_T = 4.7962 + 0.0310 (D_{BH}^2 H_t)$		(Weaver and Gillespie 1992)
All forests, *Prestoea montana* (Graham) Nichols		
$Y_T = 10.0 + 6.4 (H_t)$		(Frangi and Lugo 1985)
Subtropical wet forest		
$Y_T = \exp \{0.950 \ln (D_{BH}^2 H_t) - 3.282\}$		(Scatena et al. 1993)
$Y_T = 0.1728 (D_{BH}^2 H_t)^{0.6487}$	($D_{BH} < 5$ cm)	(Weaver and Gillespie 1992)
$Y_T = -0.1106 + 0.02991 (D_{BH}^2 H_t)$	($D_{BH} \geq 5$ cm)	(Weaver and Gillespie 1992)
$Y_T = \exp \{-3.3012 + 0.9439 \text{ in } (D_{BH}^2 H_t)\}$		(Brown et al. 1989)
$Y_T = 21.297 - 6.953 (D_{BH}) + 0.740 (D_{BH}^2)\}$		(Brown 1997)
Subtropical moist forest		
$Y_T = \exp \{-1.59 + 0.77 \ln (D_{BH}^2 H_t)\}$		(Weaver 1994)
$Y_T = \exp \{-3.1141 + 0.9719 \ln (D_{BH}^2 H_t)\}$		(Brown et al. 1989)
$Y_T = \exp \{-2.134 + 2.530 \ln (D_{BH})\}$		(Brown 1997)
Subtropical dry forest		
$Y_T = 34.4703 - 8.0671 (D_{BH}) + 0.6589 (D_{BH}^2)$		(Brown et al. 1989)
$Y_T = \exp \{-1.996 + 2.32 \ln (D_{BH})\}$		(Brown 1997)
$Y_T = 10\text{^} \{-0.5352 + \log_{10} (BA)\}$		(Martínez-Yrízar et al. 1992)*

*Aboveground biomass estimates from the (Martínez-Yrizar et al. 1992) equation do no include leaf biomass.

data sets that fell in lower montane rain forest according to the GIS life zone map, and both the plots had considerable overlap in species composition, so data from the single lower montane rain forest plot was pooled with the 6 lower montane wet forest AGB averages for a single lower montane rain/wet AGB average. This was a compromise solution necessary until better sampling of lower montane wet and rain forests allows for improved AGB estimates. The equation from Frangi and Lugo (1985) was used to estimate sierra palm (*P. montana*) AGB in all life zones (Table 1).

Subtropical wet forest equations.—Dacryodes excelsa Vahl., *Sloanea berteriana* Choisy, *Manilkara bidentata* (A.DC.) are species indicative of the tabonuco forest type, a major association within the subtropical wet forest life zone (Ewel and Whitmore 1973). *Cecropia peltata* L., *Schefflera morototoni* (Aubl.) Maguire and *Ochroma lagopus* Sw. are also common in wet forest stands at early stages of succession or recovery from disturbance (Ewel and Whitmore 1973). In areas where wet forest has been converted to shade coffee plantations, particularly in the Central Cordillera region, species such as *Guarea guidonia* (L.) Sleumer, *Inga laurina* (Sw.) Willd., *Inga vera* Willd., and *Erythrina poeppigiana* (Walp.) O.F. Cook are commonly found (Birdsey and Weaver 1982; Franco et al. 1997).

Scatena et al. (1993) estimated total AGB for trees of the Bisley Experimental watershed with diameters ranging from 2.5-57 cm in two, 32 x 32 m plots (Table 1). This data was supplemented by additional data from Ovington and Olson (1970) to develop equations from a total of 101 trees from 37 species in the tabonuco forest type. The authors developed equations for 23 species plus 2 genera and 2 groupings of structurally similar species (Scatena et al. 1993).

Weaver and Gillespie (1992) also used the Ovington and Olson (1970) data set with additional sampling to develop separate regression equations for trees with $D_{BH} < 5$ cm and $D_{BH} \geq 5$ cm for the tabonuco forest type within a D_{BH} range of 0.3-45.7 cm (Table 1). Brown et al. (1989) and the updated Brown (1997) present regression equations that use D_{BH} and H_t for subtropical and tropical wet forest based on data sets from Costa Rica, New Guinea, and Puerto Rico (the Ovington and Olson (1970) data set) using 176 trees with D_{BH} that ranged from 3.6 to 116 cm (Table 1).

Subtropical moist forest equations.—The subtropical moist forest life zone is the most extensive on Puerto Rico (Ewel and Whitmore 1973) and covers a wide variety of soil parent materials and topographic classes. This life zone is also the most heavily impacted by human activities due to its suitability for agricultural and urban development (Helmer et al. 2002; Lopez et al. 2001). These factors have resulted in highly diverse mix of native and introduced species that typically includes *Tabebuia heterophylla* (DC.) Britton, *Spathodea campanulata* Beauv., *Roystonea borinquena* O. F. Cook, *Mangifera indica* L., and species of the *Nectandra*, *Ocotea*, and *Coccoloba* genera (Ewel and Little 1973; Birdsey and Weaver 1982; Franco et al. 1997).

The only equations for the subtropical moist forest life zone developed in the Caribbean are presented in Weaver (1994) (Table 1). These equations are derived from trees in the subtropical moist forests of Puerto Rico and the US Virgin Islands. Thirteen trees in Puerto Rico's Cambalache Commonwealth Forest and 7 trees from Cinnamon Bay, St. John, US Virgin Islands, ranging from 6.0-40.5 cm D_{BH} were sampled to develop separate equations for each site and one equation using data from both sites that predicts AGB from D_{BH} and H_t measurements. We decided to use the equation developed from data from both sites for this comparison (Table 1) because; both samples are quite small, and, a preliminary analysis indicated that the combined and separate equations produced similar results.

Estimates from the equation developed in the Caribbean can be compared to estimates from two equations developed globally, the subtropical moist tropical forest equations from Brown et al. (1989) that included H_t, and an equation from Brown (1997) which only uses D_{BH} developed from 5 data sets from 224 Brazilian and Southeast Asian trees with D_{BH} ranging from 5.0-148.0 cm.

Subtropical dry forest equations.—*Bursera simaruba* (L.) Sarg., *Bucida burceras* L., *Cephalocereus royenii* (L.) Britton, and *Guaiacum officinale* L. are species commonly associated with Puerto Rican dry forest (Ewel and Whitmore 1973). The more heavily-disturbed dry forest areas have numerous, smaller stemmed *Leucaena leucocephala* (Lam.) deWit, *Prosopis juliflora* (Sw.) DC., *Acacia macracantha* Humb. & Bonpl. and *Acacia farnesiana* (L.) Willd. individuals.

No regression equations for estimating AGB in Puerto Rico's subtropical dry forests have been developed, so estimates were made using three equations developed from other data sets including the following: Brown et al. (1989), Brown (1997), and Martínez-Yrízar et al. (1992) which uses tree basal area (Table 1). Brown et al. (1989) and Brown (1997) combined 2 datasets from India of 29 trees with D_{BH} ranging from 3.7-39.2 cm, and the author states that these equations should be used for subtropical dry forest in zones with rainfall > 900 mm/yr (Brown 1997). Brown (1997) recommends using an equation from Martínez-Yrízar et al. (1992) for subtropical dry forests in zones with rainfall < 900 mm/yr. Martínez-Yrízar et al. (1992) harvested 191 trees with D_{BH} ranging from 3 cm to 44.9 cm in a single 1000 m^2 plot in dry tropical deciduous forest in Mexico. However, their equation does not include leaf biomass (Martínez-Yrízar et al. 1992). Forests classified as subtropical dry in Puerto Rico occur in areas with rainfall that ranges from 600-1400 mm/yr (Ewel and Whitmore 1973), so AGB estimates were made with all three equations.

Aboveground biomass estimates by life zone

Stem density (stems/ha), basal area (m^2/ha), and per hectare AGB (Mg/ha) were calculated for each plot and then averaged over each forested life zone, and for the different soil substrates within each life zone. Estimates from the FIA data include all stems with $D_{BH} \geq 2.5$ cm, even though the equations developed in Brown et al. (1989), Brown (1997), and Weaver (1994) are only meant for application to stems with $D_{BH} \geq 5.6$ cm. Individual tree AGB estimates were calculated for 10 cm diameter classes with each available equation, and graphed to examine model performance with increasing tree size.

The RGA watershed inventory data set

only includes trees with $D_{BH} \geq 10.0$ cm. We explore the implications of excluding these saplings by estimating the percentage of AGB in the FIA data set in trees with $D_{BH} \geq 10.0$ cm and trees with $D_{BH} < 10.0$ cm. For simplicity's sake, we estimated AGB using each of the potential regression equations, and then the multiple estimates were averaged for a single value. For example, the AGB estimate for subtropical dry forest using the Brown et al. (1989) equation was 55.27 Mg/ha, from Brown (1997) it was 22.19 Mg/ha, and from Martínez-Yrízar et al. (1992) it was 21.48 Mg/ha, which gave an average of 32.98 Mg/ha.

Field crews from both inventories used identical criteria to categorize stands as recent reversions to forest (< 10% canopy coverage in tree species), young secondary forest, and mature secondary forest. Categorizations of young versus mature secondary forest were subjective crew decisions based on the density of larger trees, species encountered, and other overall impressions of the stand. Crews did not attempt to collect detailed stand histories. We calculated stem density, basal area and AGB for these stand development categories in each life zone.

We assess the influence of larger trees ($D_{BH} \geq 50$ cm in lower montane wet/rain forest and subtropical dry forest, $D_{BH} \geq 90$ cm in subtropical wet and subtropical moist forest) on AGB estimates at the plot level and at the landscape level. First, we examined FIA plots with and without large trees separately, estimating mean stem density, basal area, and AGB values for 5 lower montane wet/rain forest, 1 subtropical dry forest, 8 subtropical wet forest and 3 subtropical moist forest plots, and then calculating the percentage contribution of the larger trees in the individual plots where they occurred. Then we calculated overall mean stem density, basal area and AGB for each entire life zone using all the FIA plots, but without large trees. The mean values from data without large trees were compared to mean values from FIA data with large trees using paired t-tests in the Statistical Analysis System (SAS) software (pages 51-52 in Freund and Littel 1981).

RESULTS

AGB estimates, forest structure, and model comparison

Average AGB, stem density, and basal area for lower montane wet, subtropical wet, subtropical moist and subtropical dry Puerto Rican forests for all trees with $D_{BH} \geq 2.5$ cm as calculated from the FIA islandwide inventory data appear in Table 2. The forests were on soils derived from: alluvium and other unconsolidated material; extrusive and intrusive volcanic parent materials; limestone and carbonate rocks; sedimentary, non-carbonate rocks; and ultramaphic parent materials (Table 2).

Averages for all trees with $D_{BH} \geq 10.0$ cm in lower montane wet, subtropical wet and subtropical moist forests found in the RGA watershed appear in Table 3. Figures 1a-d have mean individual tree AGB estimates by 10 cm tree D_{BH} classes for each forested life zone using data from the two combined forest inventory data sets, by the regression equation used to make the estimate. There were only two lower montane wet forest trees with greatly different AGB estimates in the 70 cm D_{BH} class which resulted in the very large standard error for that class (Fig. 1a). This was also the case in subtropical moist forest trees in the $D_{BH} > 100$ cm class. No standard error was calculated for subtropical dry forest trees in the 70 cm D_{BH} class because only one tree of that size was found by the FIA inventory.

In the subtropical wet forest life zone, AGB estimates derived from using the Brown (1997) were 45.2% and 28.8% higher than those derived from the locally-developed equations of Scatena et al. (1993) and Weaver and Gillespie (1992), respectively. Individual tree AGB estimates began diverging when D_{BH} reached 60-70 cm, and became erratic in the 90 cm and above D_{BH} classes. Subtropical moist forest AGB trends were similar to those in subtropical wet forest, with Brown (1997) giving AGB estimates that were 50.7% greater than those from Weaver (1994). Individual tree AGB began to diverge at the 70-80 cm D_{BH} classes. Brown et al. (1989) and Brown (1997) gave consistently higher AGB esti-

TABLE 2. Number of plots (N), mean stem density (trees/ha with $D_{BH} \geq 2.5$ cm/ha), mean basal area (m^2/ha) and mean aboveground biomass (Mg/ha) estimated from the 2001-2003 island-wide Puerto Rico forest inventory by life zone, substrate (AU = alluvium and other unconsolidated; VE = volcanic, extrusive; VI = volcanic, intrusive; LC = limestone and carbonate rocks; SD = sedimentary, non-carbonate; UM = ultramaphic), and published source of the regression equation used to calculate AGB. Standard error of the mean appears in parenthesis after each mean value. Value of N = 0 means there were no inventory plots in that forest/substrate category.

Lower montane wet forest	Grand mean	AU	VE	VI	LC	SD	UM
N	7	0	5	2	0	0	0
Trees/ha	2551.21 (396.89)	—	2643.58 (558.66)	2320.27 (335.06)	—	—	—
BA (m^2/ha)	26.47 (4.31)	—	23.76 (5.70)	33.26 (0.64)	—	—	—
AGB (Weaver and Gillespie 1992)	116.9 (27.68)	—	88.86 (30.39)	186.63 (5.17)	—	—	—
Subtropical wet forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	68	0	49	11	2	2	4
Trees/ha	2717.25 (177.27)	—	2882.90 (235.96)	1913.65 (269.40)	2961.28 (819.12)	2011.81 (1132.62)	2564.35 (524.56)
BA (m^2/ha)	27.67 (2.73)	—	30.66 (3.78)	18.74 (3.68)	19.05 (3.08)	30.77 (3.30)	14.80 (5.63)
AGB (Weaver and Gillespie 1992)	146.39 (15.54)	—	162.62 (20.89)	90.14 (23.18)	81.74 (17.51)	215.43 (45.60)	68.97 (34.11)
AGB (Scatena et al. 1993)	111.50 (11.00)	—	123.27 (14.73)	70.99 (17.02)	68.09 (14.04)	143.58 (12.76)	54.79 (26.29)
AGB (Brown et al. 1989)	103.17 (10.08)	—	113.93 (13.48)	65.93 (15.65)	63.61 (13.03)	132.78 (11.85)	51.07 (24.26)
AGB (Brown 1997)	174.80 (22.51)	—	199.77 (31.53)	109.12 (26.53)	92.14 (20.50)	187.99 (3.25)	81.30 (37.48)
Subtropical moist forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	136	12	51	13	58	0	2
Trees/ha	3401.64 (206.47)	3600.23 (538.16)	3173.79 (335.58)	3123.60 (721.82)	3565.23 (329.13)	—	5083.15 (1804.00)
BA (m^2/ha)	20.56 (1.21)	23.62 (3.78)	19.71 (1.71)	20.49 (3.11)	21.07 (2.18)	—	9.51 (2.81)
AGB (Weaver 1994)	91.61 (5.75)	102.35 (16.09)	85.16 (7.48)	84.29 (11.77)	98.51 (10.94)	—	39.29 (15.31)
AGB (Brown et al. 1989)	113.20 (9.08)	128.36 (29.00)	100.32 (10.65)	107.48 (18.30)	125.72 (17.59)	—	24.27 (9.79)
AGB (Brown 1997)	162.81 (14.02)	195.44 (48.11)	147.72 (16.63)	173.94 (37.94)	171.14 (26.45)	—	37.60 (10.49)
Subtropical dry forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	24	3	7	0	14	0	0
Trees/ha	4173.77 (481.61)	3158.12 (1971.07)	3653.95 (451.13)	—	4651.32 (695.33)	—	—
BA (m^2/ha)	11.63 (1.49)	16.23 (5.63)	11.58 (2.34)	—	10.66 (2.00)	—	—
AGB (Brown et al. 1989)	76.49 (8.86)	102.41 (38.96)	60.39 (7.04)	—	78.98 (12.45)	—	—
AGB (Brown 1997)	43.73 (7.52)	78.68 (42.33)	41.06 (9.58)	—	37.57 (8.24)	—	—
AGB (Martínez-Yrizar et al. 1992)	33.93 (4.35)	47.38 (16.46)	33.80 (6.84)	—	31.11 (5.84)	—	—

TABLE 3. Number of plots (N), mean stem density (trees/ha with $D_{BH} \geq 10.0$ cm/ha), mean basal area (m^2/ha), and mean aboveground biomass (Mg/ha) estimated from the 2003 Rio Grande de Arecibo forest inventory by life zone, substrate (AU = alluvium and other unconsolidated; VE = volcanic, extrusive; VI = volcanic, intrusive; LC = limestone and carbonate rocks; SD = sedimentary, non-carbonate; UM = ultramaphic), and published source of the regression equation used to calculate AGB. Standard error of the mean appears in parenthesis after each mean value. Value of N = 0 means there were no inventory plots in that forest/substrate category.

Lower montane wet forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	4	0	0	1	0	3	0
Trees/ha	585.00 (218.54)	—	—	230.00 (–)	—	703.33 (259.83)	—
BA (m^2/ha)	22.78 (8.08)	—	—	4.57 (–)	—	28.85 (7.53)	—
AGB (Weaver and Gillespie 1992)	63.44 (22.60)	—	—	11.30 (–)	—	80.82 (20.42)	—
Subtropical wet forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	47	0	7	14	2	24	0
Trees/ha	450.85 (25.56)	—	461.43 (67.42)	358.57 (28.51)	290.00 (120.00)	515.00 (37.46)	—
BA (m^2/ha)	21.54 (1.17)	—	22.63 (3.64)	20.52 (2.05)	16.21 (9.58)	22.25 (1.58)	—
AGB (Weaver and Gillespie 1992)	83.57 (5.10)	—	78.25 (10.63)	83.97 (10.14)	74.31 (51.21)	85.66 (7.00)	—
AGB (Scatena et al. 1993)	65.50 (3.82)	—	61.22 (8.21)	64.74 (7.27)	57.60 (38.85)	67.86 (5.33)	—
AGB (Brown et al. 1989)	60.73 (3.52)	—	56.70 (7.60)	59.86 (6.66)	53.28 (35.84)	63.03 (4.93)	—
AGB (Brown 1997)	142.93 (8.58)	—	153.89 (25.39)	142.79 (16.68)	110.15 (68.90)	142.55 (11.17)	—
Subtropical moist forest	Grand Mean	AU	VE	VI	LC	SD	UM
N	8	0	0	6	0	2	0
Trees/ha	533.75 (44.64)	—	—	521.67 (59.52)	—	570.00 (30.00)	—
BA (m^2/ha)	18.10 (2.61)	—	—	16.60 (3.07)	—	22.57 (4.78)	
AGB (Weaver 1994)	65.14 (10.05)	—	—	58.67 (8.47)	—	84.56 (35.35)	—
AGB (Brown et al. 1989)	84.17 (15.23)	—	—	74.50 (11.66)	—	113.16 (57.72)	—
AGB (Martínez-Yrizar et al. 1992)	154.88 (26.50)	—	—	142.69 (32.02)	—	191.46 (49.99)	—

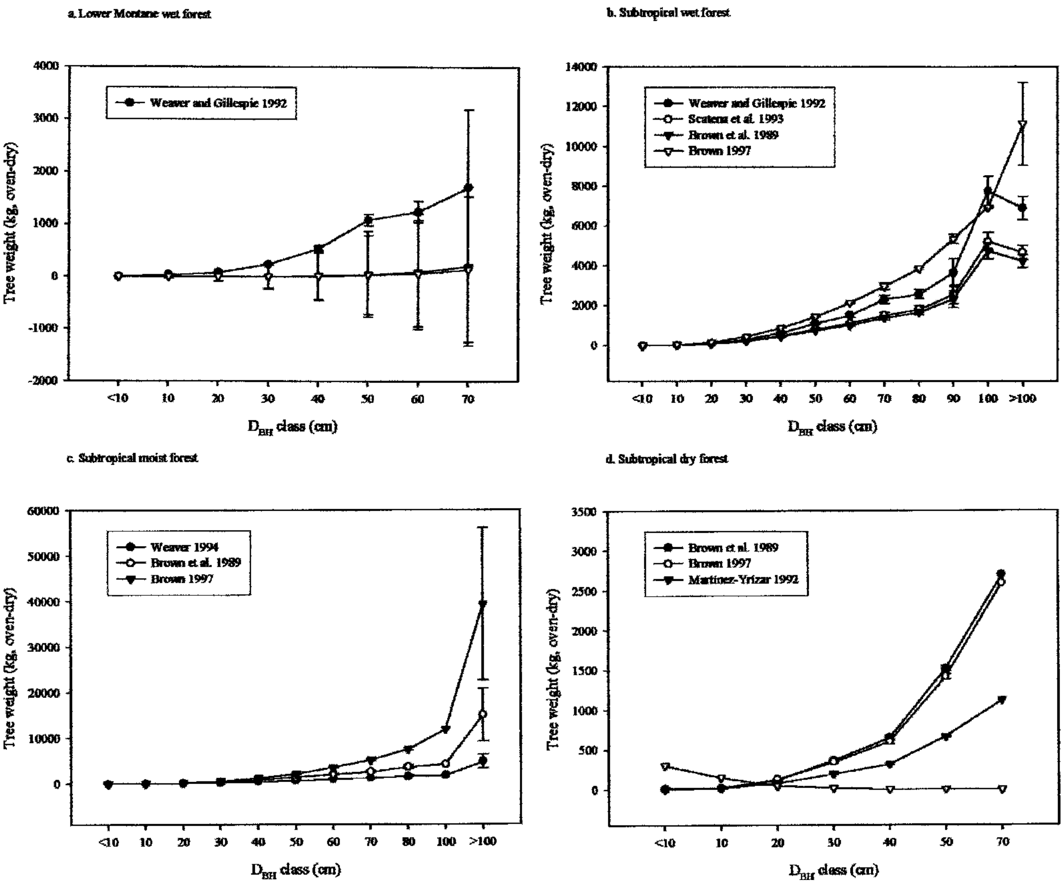


FIG. 1. Mean individual tree aboveground biomass (oven-dry kg) in 10 cm D_{BH} classes, by forested life zone, with standard errors. (Note different Y-axis scales)

mates (55.6% and 22.4%, respectively) than did the Martínez-Yrízar et al. (1992) equation in subtropical dry forests. Martínez-Yrízar et al. (1992) does not take into account leaf biomass, but estimates from their equation are still lower than those from the Brown equations because leaf biomass in the Mexican subtropical dry deciduous forests only accounted for an additional 5% of the total live tree biomass (Martínez-Yrízar et al. 1992).

Stand development and AGB

Figures 2 a-c show stem density, basal area, and AGB for all trees with $D_{BH} \geq 2.5$ cm as calculated from the FIA island-wide inventory data for each of the three stand development stages categorized by the field crews. Data from the RGA inventory were not used to assess successional stages because it could not account for stems with $D_{BH} < 10$ cm which were deemed important to describing young stands. We were unable to test successional differences in mature subtropical dry forest owing to small sample size.

To better assess the range, frequency, and distribution of AGB values found across the Puerto Rican landscape, the frequency distributions of FIA inventory plot AGB estimates were graphed for subtropical wet, moist and dry forests (Figs. 3 a-c). Lower montane wet forest was not graphed because there were only 4 plots in the FIA inventory data that fell in that life zone.

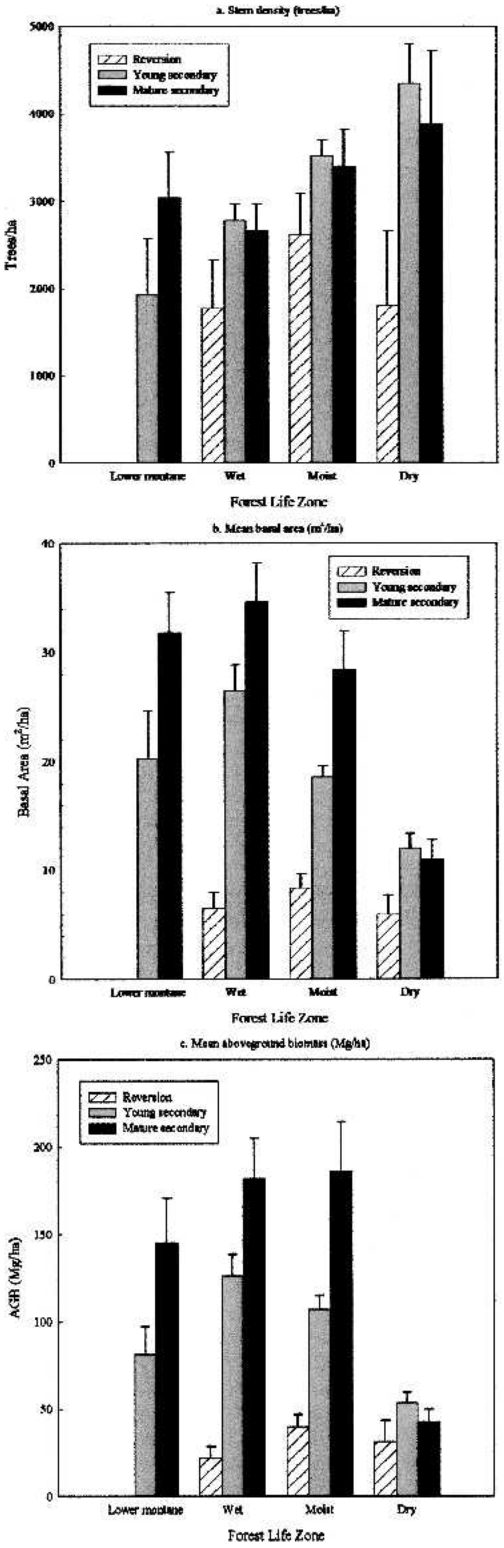


FIG. 2. Mean stem density (trees/ha with $D_{BH} \geq 2.5$ cm/ha), mean basal area (m^2/ha), and mean aboveground biomass (Mg/ha) estimated from the 2001-2003 island-wide Puerto Rico forest inventory by life zone for each of the three stand development stages categorized by the field crews. Error bars represent standard error of the mean values.

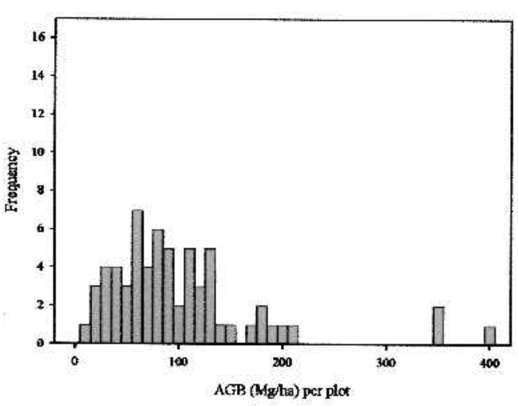
AGB in small ($D_{BH} < 10$cm) and large ($D_{BH} > 50$-90 cm) trees

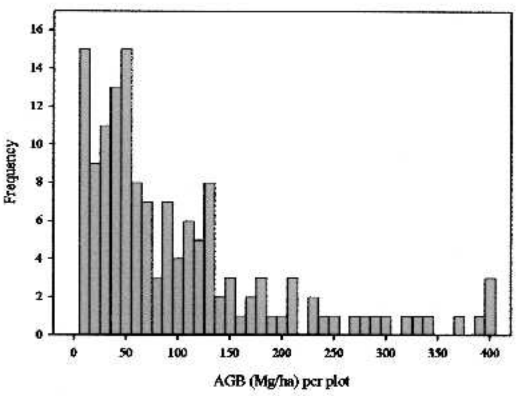
To illustrate the importance of saplings, figure 2 presents the percent contribution made by trees with $D_{BH} \leq 10$ cm to forest AGB, stem density and basal area. Only the FIA inventory data was used for this figure to account for the contribution of trees with $D_{BH} < 10$ cm to overall site AGB. The contribution of trees with $D_{BH} < 10.0$ cm ranged from a high of 50.9% of the AGB, 63.3% of the basal area and 94.5% of the stem density in subtropical dry forest to a low 9.9% of the total AGB and 18.6% of the total basal area in subtropical wet forest (Fig. 4).

Trees with $D_{BH} \geq 90$ cm contributed 54-62% of the AGB when they were encountered in subtropical wet forest inventory plots, and 78-84% of the AGB at the one subtropical dry forest inventory plot that had trees with $D_{BH} \geq 50$ cm (Table 4). However, paired t-tests did not find statistically significantly differences (indicated by a Pr > t statistic of 0.05) in mean stem density, basal area, or AGB values for any life zone when comparing averages from the FIA data set with and without larger trees, indicating that there were too few inventory plots with large trees to have an effect on landscape-level estimates of those values (Fig. 5).

DISCUSSION

First, we discuss how AGB, stem density and basal area estimates from the forest inventory data compare to estimates in the published literature about Puerto Rico's forests, by life zone (Table 5). Then, we address the effects of stand development and succession on AGB and the influence that many small stems ($D_{BH} < 10$ cm) and few


a. Subtropical wet forest


b. Subtropical moist forest

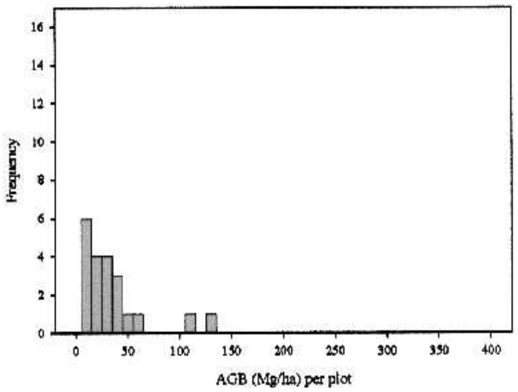

c. Subtropical dry forest

FIG. 3. Frequency distribution of aboveground biomass (AGB) estimates from the 2001-2003 island-wide Puerto Rico forest inventory for subtropical wet, subtropical moist, and subtropical dry forest life zones. (Note that lower montane wet forest is not graphed due to the small number of plots present.)

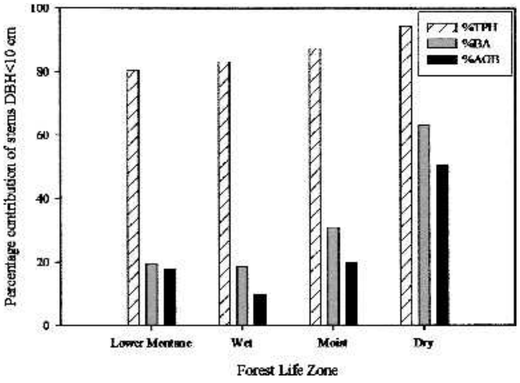


FIG. 4. Percentage of total aboveground biomass (AGB), stem density (TPH), and basal area (BA) in stems with D_{BH} < 10 cm, by life zone.

large stems (D_{BH} > 50-90 cm) has on plot and landscape-level AGB estimates.

Lower montane rain/wet forest

Puerto Rican subtropical lower montane wet/rain forest AGB estimates from these two forest inventories (116.79 Mg/ha from FIA and 63.44 Mg/ha from RGA) fall within the range of values found in previous studies. Weaver (1987) estimated AGB using the equations developed by Crowe (1978) for plots in the elfin cloud forest in the Luquillo mountains. One plot on the ridge had 48 Mg/ha, while the leeward slope plot had 110 Mg/ha. Weaver (1990), again working in elfin forest, found 235.1 Mg/ha of AGB in dicotyledonous trees and shrubs, and 97.5 Mg/ha in palms. Weaver (2000) used the equations developed by Wadsworth (1949) and Weaver (1987) to estimate AGB in the palo colorado forest type where the average AGB was 148.2 Mg/ha.

Subtropical wet forest

The subtropical wet forest AGB estimates of 103.17-174.80 Mg/ha made using the FIA data and 60.73-142.93 Mg/ha for stems with $D_{BH} \geq 10.0$ cm in the RGA fall within the lower range of values found in published studies. This might be in part due to the island-wide FIA survey's inclusion of subtropical wet forests on ultramaphic parent materials, which showed lower than av-

TABLE 4. Mean stem density (number of trees with $D_{BH} \geq 2.5$ cm/ha), mean basal area (m^2/ha), and mean aboveground biomass (Mg/ha) in all stems, and trees with $D_{BH} < 50$ cm (lower montane wet and dry forests) and $D_{BH} < 90$ cm (moist and wet forests) D_{BH} stems, and the percentage contribution of trees ≥50 or 90 cm to each, by life zone and published source of the regression equation used to calculate AGB. (Note data from island-wide Puerto Rico forest inventory only, and only plots which contained trees with trees ≥50 or 90 cm).

Lower montane wet forest (N = 5 plots)

	Equation source	All trees	Only trees $D_{BH} < 50$ cm	% contribution $D_{BH} \geq 50$ cm
Tree/ha	—	2873.93	2870.94	0.10
BA (m^2/ha)	—	32.38	31.35	3.17
AGB/ha	(Weaver and Gillespie 1992)	142.90	142.22	0.48

Subtropical dry forest (N = 1 plot)

	Equation source	All trees	Only trees $D_{BH} < 50$ cm	% contribution $D_{BH} \geq 50$ cm
Tree/ha	—	922.14	842.49	8.64
BA (m^2/ha)	—	27.47	6.14	77.64
AGB/ha	(Brown et al. 1989)	175.73	31.15	82.28
	(Brown 1997)	163.24	26.75	83.62
	(Martínez-Yrízar et al. 1992)	80.23	17.93	77.64

Subtropical wet forest (N = 8 plots)

	Equation source	All trees	Only trees $D_{BH} < 90$ cm	% contribution $D_{BH} \geq 90$ cm
Tree/ha	—	3195.41	3165.54	0.93
BA (m^2/ha	—	66.04	30.42	53.94
	(Weaver and Gillespie 1992)	387.34	164.52	57.53
	(Scatena et al. 1993)	275.85	125.67	54.44
	(Brown et al. 1989)	252.75	116.20	54.03
	(Brown 1997)	506.43	194.6	61.56

Subtropical moist forest (N = 3 plots)

	Equation source	All trees	Only trees $D_{BH} < 90$ cm	% contribution $D_{BH} \geq 90$ cm
Tree/ha	—	2369.64	2353.05	0.70
BA (m^2/ha)	—	51.55	26.21	49.16
AGB/ha	(Weaver 1994)	172.35	104.52	39.35
	(Brown et al. 1989)	347.52	141.67	59.24
	(Brown 1997)	788.56	244.39	69.01

erage AGB and basal areas. Estimates of AGB for subtropical wet and rain forest life zone within the Caribbean National Forest range from 110.3 Mg/ha (Scatena et al. 1993) to 285.0 Mg/ha (Weaver 1998). Ovington and Olson's (1970) study found an average of 198.1 Mg/ha of AGB in subtropical wet forests. Weaver (1998) tracked AGB change in relation to hurricane disturbance. Working in a mix of tabonuco, palo colorado and palm forest sites that were impacted by Hurricane Hugo, Weaver (1998) calculated that the sites held 232 Mg/ha in 1946, 285 Mg/ha in 1988, and decreased to 237 Mg/ha in 1991 (pos.—hurricane Hugo). Aide et al. (2000) estimated AGB at sites in Carite, Ciales, Luquillo and Utuado using the equations from Weaver and Gillespie (1992) to arrive at an estimates of 165-220 Mg/ha of AGB in 70+ year-old secondary subtropical wet and rain forests.

In the Bisley Experimental watershed of the Caribbean National Forest where the AGB work of Scatena et al. (1993) was performed, human impacts have been relatively slight compared to other forested areas of the island. Basal areas there ranged from 22.52-28.02 m^2/ha (Dallmeier et al. 1998). Studies from outside the Caribbean

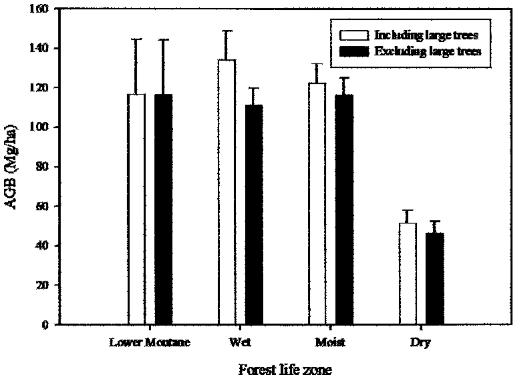


FIG. 5. Mean aboveground biomass (Mg/ha) including and excluding large trees ($D_{BH} \geq$ 50cm in lower montane wet/rain and dry forest, $D_{BH} \geq$ 90cm in subtropical wet and moist forest), with standard errors of the mean, by forested life zone.

National Forest are fewer, but those that have been carried out provide valuable insight into the disturbed, secondary forests that predominate on the Puerto Rican landscape. Wide variation in stand structural characteristics reflects the varying degrees of disturbance and differences in land use history. In inventory plots outside of public forests, Birdsey and Weaver (1982) found 13.8 m^2/ha basal area on subtropical wet and subtropical moist forest in 1980, and Franco et al. (1997) found 15.1 m^2/ha in 1990. Aide et al. (2000) found 30-39 m^2/ha of basal area on sites in Carite, Ciales, Luquillo and Utuado. Popper et al. (1999), working in secondary forests in the area of Utuado and Barranquitas, found basal areas that averaged 17.9-39.8 m^2/ha and 1680-1,124 stems/ha for tree species with D_{BH} > 4 cm. Marcano-Vega et al. (2002) studied abandoned coffee shade and pastures in the central Cordillera where basal areas were found to range from 9.8-49.5 m^2/ha in 6,070 to 12,880 stems/ha with D_{BH} > 1 cm in abandoned coffee shade, and 4.2-32.3 m^2/ha in 3,200 to 9,460 stems/ha with D_{BH} > 1 cm in abandoned pasture sites.

Subtropical moist forest

The wide range of subtropical moist forest structural characteristics, which have

TABLE 5. Previously published estimates of total woody aboveground biomass (Mg/ha) for the major forested life zones of Puerto Rico.

Source	Location	Forest type	Holdridge Life zone	AGB (Mg/ha)
(Frangi and Lugo 1985)	Luquillo	palm	Lower montane wet forest and rain forest	174
(Weaver et al. 1986)	Luquillo	elfin	Lower montane rain forest	48-110
(Weaver 1987)	Luquillo	palo colorado	Lower montane wet forest and rain forest	121-145
(Weaver 1990)	Luquillo	elfin	Lower montane rain forest	332.6
(Weaver and Murphy 1990)	Luquillo	palo colorado	Lower montane wet forest	130
(Weaver 1998)	Luquillo	tabonuco, palo colorado and palm	Subtropical wet forest, rain forest and lower montane wet forest	232-285
(Weaver 2000)	Luquillo	palo colorado	Lower montane wet forest	148
(Ovington and Olson 1970)	Luquillo	tabonuco	Subtropical wet forest	198
(Scatena et al. 1993)	Luquillo	tabonuco	Subtropical wet forest	110-221
(Aide et al. 2000)	Carite, Ciales, Utuado, Luquillo	secondary	Subtropical wet forest, rain forest and lower montane wet forest	165-220
(Silver et al. 2004)	Luquillo	secondary	Subtropical moist forest	80
(Weaver 1996)	Cinnamon Bay, St. John, USVI	secondary	Subtropical moist forest	131
(Murphy and Lugo 1986)	Guanica	dry forest	Subtropical dry forest	45

both inherent and anthropogenic causes, complicates assessing the accuracy of inventory AGB estimates. Subtropical moist forests typically occupy the lowland areas that were heavily cleared for agriculture and are now under pressure for urban development (Rudel et al. 2000; Lopez et al. 2001), leaving the remaining forest heavily disturbed or at varying stages of succession. However, stem density values and basal area in the subtropical moist forests inventoried island-wide and in the RGA watershed fall within the wide range of values found in other studies.

In subtropical moist forests on Puerto Rico, average basal areas of 32.4 m^2/ha and stem density of 4,500 stems/ha have been observed in abandoned pastures and coffee shade in the karst region (Rivera and Aide 1998). Alvarez-Ruiz (1997) found basal areas that ranged from 12.4 to 27.1 m^2/ha for 520 to 7,970 stems with $D_{BH} > 2.5$ cm in subtropical moist forest stands at varying successional stages and land use histories in the karst region. The non-karst subtropical moist forest studied by Chinea (2002) had basal areas that ranged from 10 to 30 m^2/ha in 500 to 2600 stems with $D_{BH} > 2.5$ cm per hectare. In another example of non-karst moist forest, Silver et al. (2004) found that a 55-61 year old reforested area originally planted with multiple species and colonized by naturally regenerating native species in the Luquillo Mountains had an average of 26 m^2/ha of basal area and 80 Mg/ha of AGB.

The stands surveyed by the forest inventories were generally less developed than those found by Weaver (1994, 1996) in the Cinnamon Bay Watershed in the Virgin Islands National Park on St. John where basal area ranged from 24.0-25.1 m^2/ha, stem density from 3,141-3,429 stems/ha, and AGB from 131.5-150.4 Mg/ha. Presenting AGB estimates to a common index based on Mg of AGB per square meter of basal area produces 4.46 Mg/m^2 using the Weaver (1994) equation, 5.51 Mg/m^2 from Brown et al. (1989), and 7.92 Mg/m^2 from Brown (1997). The average in Cinnamon Bay was 3.86 Mg/m^2.

Subtropical dry forest

Basal area and stem density found in these forest inventory plots were considerably less than that found by Murphy and Lugo (1986) in subtropical dry forest of the Guánica Commonwealth Forest. Basal area of all trees with $D_{BH} \geq 2.5$ cm averaged 19.8 m^2/ha for 12,173 stems/ha, and there was 44.75 Mg/ha of AGB in all living vegetation (not only in trees with $D_{BH} \geq 2.5$ cm) (Murphy and Lugo 1986). These differences in basal area and stem density are understandable because the Guánica Commonwealth Forest has suffered less human impact than the rest of the island's unprotected subtropical dry forests (Murphy and Lugo 1990). To normalize comparisons between the AGB found in the Guánica Commonwealth Forest and the AGB densities found in the FIA inventory, Murphy and Lugo (1986) found that there was 2.26 Mg of AGB per m^2 of basal area. The FIA inventory found that there were 6.58 Mg/m^2 based on the use of Brown et al. (1989) regression equation, 3.76 Mg/m^2 from the Brown (1997) equation, and 2.92 Mg/m^2 from Martínez-Yrízar et al. (1992).

Stand development and AGB

Field crews found subtropical wet forests in a wide range of successional stages with structural characteristics typical of secondary tropical forests (Table 5); high densities of smaller diameter stems and lower basal areas when compared to more mature stands (Brown and Lugo 1990), Of course, this was expected as there is some circular reasoning involved; field crews classified stands with more closed canopies and larger stems as being more mature. However, there is still value in describing the range of values found across the landscape even if we cannot directly age stands and establish temporal trends. The skewed frequency distribution of AGB estimates toward the lower end of the values found in the inventory and the infrequent occurrence of plots with much higher AGB values (Figs. 3 a-c) would indicate a predominance of younger successional stages and the potential for greater biomass accumulation over time in the subtropical wet, moist and dry forest life zones.

Subtropical moist forests accumulated basal area and AGB with maturity as would be expected, and the large number of inventory plots that fell on recently reverted forest (17%), indicates that agricultural land abandonment in the subtropical moist forest life zone continues (Figs. 2 a-c).

AGB in small (D_{BH} < 10 cm) and large (D_{BH} > 50-90 cm) trees

The proportion of forest AGB found in small trees by FIA (9.9% in subtropical wet forest, 19.9% in subtropical moist forest) was higher than that found by Chave et al. (2004) (6%) and within the broad range of values found by Schroeder et al. (1997) (10-75%) and Cummings et al. (2002) (12%). Brown (2002), based on the findings in Schroeder et al. (1997), postulates that as succession advances and stands accumulate AGB, the contribution to total AGB by trees with D_{BH} < 10 cm decreases. Based on the results of this study, it appears that the inverse relationship between the percentage of AGB in small stems and total stand AGB also holds true when comparing across forests with similar ages but of different inherent levels of productivity. Less productive subtropical dry forests with lower total AGB densities have more of their AGB in small stems than more productive subtropical wet forests with higher total AGB densities.

Aboveground biomass concentrated in a few large trees (50-90 cm D_{BH}) had the potential to greatly influence individual plot AGB densities wherever they were present (Fig. 5), an effect recognized in previous studies (Brown et al. 1995; Keller et al. 2001; Chave et al. 2004). However, our ability to accurately estimate individual tree AGB decreases with increasing diameters as seen in figures 1a-d, meaning trees with the most influence on plot level AGB estimates potentially have the least accurate individual AGB estimates.

Erratic AGB estimates for individual large trees have a number of causes. Field experience showed us that tree form often becomes more variable in the larger trees due to the accumulated damage attendant with age and stem buttressing. Hurricane-damaged crowns and reduced heights are commonly found in larger trees in Puerto Rico and many places in the Caribbean. Variance in tree heights influenced the AGB estimates coming from the different equations. The drop in estimated AGB in subtropical wet forest trees with D_{BH} > 100 cm occurs only with estimates made using equations that have height as an explanatory variable (Fig. 1b). Brown's (1997) equations for subtropical wet forest trees were developed from data sets from Costa Rica, New Guinea and Puerto Rico forests. Including the Puerto Rican data set seems to improve predictions for trees with D_{BH} < 70-80 cm, putting them more in line with predictions from equations that included height as an explanatory variable. Note that the equations for subtropical moist forest from Brown (1997) do not use height as an explanatory variable, and that the data sets used to develop these equations rely entirely on subtropical moist forest trees from continental tropical forests which are not impacted by hurricanes (Brazil and Southeast Asia), which seems to result in appreciable divergence from Weaver (1994) predictions for larger diameter trees.

Errors from extrapolating predictive models beyond the range of trees sampled to develop them seen in Nelson et al. (1999) are illustrated by the results from the Brown (1997) and Weaver and Gillespie (1992) equations which show indications of over-estimation and erratic predictions at diameters above 90 cm in subtropical wet forests (Fig. 1b). The data set from Puerto Rico used in Brown (1997) came from Ovington and Olson (1970), as did part of the Weaver and Gillespie (1992) data set, and Ovington and Olson's (1970) data do not include any trees with D_{BH} > 45.7 cm.

However, despite the influence of larger trees at the plot-level, their occurrence is sufficiently rare across the landscape that life zone-wide and island-wide estimates do not change significantly when they are excluded from the data (Fig. 5). This agrees with the argument made by Keller et al. (2001) that large trees are relatively rare on the landscape so improvement to regression equations for large trees would give minimal improvements to overall AGB estimates as compared to the potential returns on better sampling of the far more ubiquitous middle size classes (35-75 cm D_{BH}).

Conclusions

Slightly lower forest AGB estimates from broad scale forest inventories appears to be the result of including stands that have been more disturbed and are less developed than many of the stands measured in previous studies. Both forest inventories were unbiased samples of the all or portions of the Puerto Rican landscape; they did not focus on any unique forested area or forest characteristics in plot location selection. It appears likely that, even after the separation of recent forest reversions, the inventory data sets included stands at earlier stages of recovery from human disturbance than many of the previous studies of the island's forests due to objective, unbiased sampling strategies. The FIA forest inventory accurately reflects overall average forest conditions across the entire island of Puerto Rico, and the RGA inventory accurately describes the forests of that watershed. Many studies have highlighted unique characteristics, novel species assemblages, or specific land use histories that have been subjectively chosen for study. Although these studies provide much valuable information in their own right, they do not reflect average forest conditions on the island. The inventories' findings further emphasize the central role of disturbance and recovery in shaping the Puerto Rican landscape.

Applying several regression equations to the forest inventory data sets demonstrates the potential differences and estimation errors associated with the equation selection. Expanding individual tree AGB estimates to per area estimates amplifies these differences. Differing AGB estimates from using different equations appear to primarily be the result of increasing divergence in individual tree AGB estimates at larger diameters (Figs. 1a-d). Generally, AGB equations are developed using data sets which contain very few larger trees due to the difficulty in destructively sampling them. As a result, the size classes with some of the most influential and variable trees are represented by the fewest sampled individuals, a conclusion arrived at in other studies (Brown et al. 1995; Houghton et al. 2001). However, these errors are mitigated by the rareness of large trees on the Puerto Rican forest landscape.

Greater accuracy in estimating AGB in Puerto Rico's subtropical wet forest might depend on choosing between the locally-developed subtropical wet forest equations presented in Scatena et al. (1993) and those in Weaver and Gillespie (1992) based on a more detailed categorization of the forest type and careful matching on a site-by-site basis. The work of Scatena et al. (1993) took place in tabonuco forest type in the subtropical wet forest life zone, while that of Weaver and Gillespie (1992) was in the tabonuco, palo colorado, and elfin forest types of the subtropical wet and rain forest life zones. While Weaver's (1994) equations for the subtropical moist forests of Puerto Rico and the US Virgin Islands could be considered for estimating AGB for the subtropical moist karst region in northwestern Puerto Rico and for the subtropical moist forests of the US Virgin Islands, the study's small sample size and relatively low AGB estimates must be taken into consideration. Estimates derived from the Brown et al. (1989) regression equation might be preferable until additional work is done specific to local forests. For subtropical dry forest, Martínez-Yrízar et al. (1992) estimated AGB densities which were similar to those found in the subtropical dry Guánica Commonwealth Forest, which has an average annual rainfall of 860 mm (Murphy and Lugo 1986). The equations of Brown et al. (1989) and Brown (1997) could be considered for estimating AGB in subtropical dry forests with higher annual rainfalls, but with the awareness that until local regression equations for higher rainfall subtropical dry forest in the Caribbean are developed, there is the danger of over-estimating subtropical dry forest AGB. Estimating AGB in the subtropical dry forests will continue to be problematic until local regression equations are developed.

Accurate AGB estimates in Puerto Rico need to include saplings with $D_{BH} < 10$ cm because they make up a significant portion of the total AGB, particularly in lower montane, subtropical dry forests and forest in earlier successional stages. We fully agree with Brown (2002) and Clark and Clark (2000) that estimating AGB in larger trees ($D_{BH} > 80$ cm) will be erratic and imprecise until more, larger trees have been sampled and included in deriving new regression equations. Caribbean island trees appear to be of shorter stature when mature than trees in other tropical forests perhaps due to adaptation to, or damage from, hurricanes. Because of this, regression equations that use height need to be based on Caribbean tree heights rather than continental tropical tree heights to be accurate in the Caribbean.

Acknowledgments.—I would like to thank Eileen Helmer of the USDA-FS International Institute of Tropical Forestry for her assistance with GIS coverages, facilitation of data collection, and comments on this manuscript; James Rosson of the USDA-FS Southern Research Station, Joseph Donnegan of USDA-FS Pacific Northwest Research Station, and Danilo Chinea of the University of Puerto Rico at Mayagüez for their comments on the manuscript; the Puerto Rican Conservation Foundation and Citizens for the Karst for their assistance in the joint effort of collecting the FIA inventory data; Jonathan Buford, Johanna D'Arcy, Orlando Díaz, Christopher Furr, Jeremy Grayson, Humfredo Marcano, Omar Monsegur, Luis Ortíz, Humberto Rodriguez, Jim Schiller and Iván Vicéns for their tireless efforts in the field; and Luis R. Pérez Alegría of the Department of Agricultural and Biosystems Engineering, University of Puerto Rico at Mayagüez, and PI of the Atmospheric Carbon Sequestration Project of the UPRM-NASA-URC, for his assistance with data collection and analysis of the Río Grande de Arecibo watershed data. We would also like to thank T. Mitchell Aide and an anonymous reviewer for their reviews and suggestions.

LITERATURE CITED

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8:328-338.

Alvarez-Ruiz, M., P. Acevedo-Rodríguez, and M. Vázquez. 1997. Quantitative description of the structure and diversity of the vegetation in the limestone forest of Río Abajo, Arecibo-Utuado, Puerto Rico. *Acta Científica* 11:21-66.

Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. General Technical Report WO-59, USDA Forest Service, Washington, D.C.

Birdsey, R. A., and P. L. Weaver. 1982. The forest resources of Puerto Rico. Resource Bulletin SO-85, USDA Forest Service Southern Forest Experiment Station, New Orleans, Louisiana.

Brandeis, T. J. 2003. Puerto Rico's Forest Inventory: Adapting the Forest Inventory and Analysis Program to a Caribbean Island. *Journal of Forestry* 101: 8-13.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. C. Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests: An example from Rondonia, Brazil. *Forest Ecology and Management* 75:175-189.

Brown, S. 1997. Estimating biomass and biomass change in tropical forests. A primer. FAO Forestry Paper 134, Food and Agriculture Organization of the United Nations, Rome.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges. *Environmental Pollution* 116:363-372.

Brown, S., A. J. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with application to forest inventory data. *Forest Science* 35:881-902.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1-32.

Brown, S., and A. E. Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia* 17:8-18.

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

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao, and R. Perez. 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society: Biological Sciences* 359:409-420.

Chinea, J. D. 2002. Tropical forest succession on abandoned farms in the Humacao Municipality of eastern Puerto Rico. *Forest Ecology and Management* 167: 195-207.

Clark, D. B., and D. A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* 137: 185-198.

Cost, N. D., and J. P. McClure. 1982. Multiresource Inventories: Techniques for estimating biomass on a statewide basis. Research Paper SE-228, USDA Forest Service, Southeastern Forest Experimental Station, Asheville, NC.

Crowe, T. R. 1978. Common regressions to estimate tree biomass in tropical stands. *Forest Science* 24: 110-114.

Cummings, D. L., J. B. Kauffman, D. Perry, and R. F. Hughes. 2002. Aboveground biomass and structure of rainforests in the southwestern Brazilian Amazon. *Forest Ecology and Management* 163:293-307.

Dallmeier, F., J. A. Comiskey, and F. N. Scatena. 1998. Five years of forest dynamics following hurricane Hugo in Puerto Rico's Luquillo Experimental Forest. In *Forest biodiversity in North, Central and South America and the Caribbean. Research and Monitoring*. ed. F. Dallmeier and J. A. Comiskey, 231-248. Washington, D. C.: Parthenon Publishing Group.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263:185-190.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the US Virgin Islands. Research Paper ITF-18, USDA Forest Service Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Francis, J. K., and H. A. Liogier. 1991. Naturalized exotic tree species in Puerto Rico. General Technical Report SO-82, USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Franco, P. A., P. L. Weaver, and S. Eggen-McIntosh. 1997. Forest resources of Puerto Rico, 1990. Southern Resource Bulletin SRS-22, USDA Forest Service Southern Research Station, Asheville, North Carolina.

Frangi, J. L., and A. E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs* 55:351-369.

Freund, R., J., and R. C. Littel. 1981. SAS for linear models. A guide to the ANOVA and GLM procedures. SAS Institute Inc., Cary, NC.

Grau, R. H., T. M. Aide, J. K. Zimmerman, and J. R. Thomlinson. 2004. Trends and scenarios of the carbon budget in post-agricultural Puerto Rico (1936-2060). *Global Change Biology* 10:1163-1179.

Helmer, E. H., O. Ramos, T. del Mar-López, M. Quiñones, and W. Diaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean Biodiversity Hotspot. *Caribbean Journal of Science* 38:165-183.

Houghton, R. A., K. T. Lawrence, J. L. Hackler, and S. Brown. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology* 7:731-746.

Houghton, R. A., D. L. Skole, C. A. Nobre, J. L. Hackler, K. T. Lawrence, and W. H. Chomentowski. 2000. Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* 403:301-304.

Keller, M., M. Palace, and G. Hurtt. 2001. Biomass estimation in the Tapajos National Forest, Brazil: Examination of sampling and allometric equations. *Forest Ecology and Management* 154:371-382.

Little, E. L., R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. Agriculture Handbook No. 449, USDA Forest Service, Washington, D.C.

López, T. d. M., T. M. Aide, and J. R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio* 30:49-54.

Lugo, A. E., and E. H. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190:145-161.

Marcano-Vega, H., T. M. Aide, and D. Báez. 2002. Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. *Plant Ecology* 161:75-87.

Martínez-Yrízar, A., J. Sarukhán, A. Pérez-Jiménez, E. Rincón, M. Maass, A. Solís-Magallanes, and L. Cervantes. 1992. Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México. *Journal of Tropical Ecology* 8:87-96.

Murphy, P. G., and A. E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* 18:89-96.

Murphy, P. G., and A. E. Lugo. 1990. Dry forests of the tropics and subtropics: Guanica forest in context. *Acta Científica* 4:15-24.

Nascimento, H. E. M., and W. F. Laurance. 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management* 168:311-321.

Nelson, B. W., R. Mesquita, J. L. G. Pereira, S. Garcia Aquino de Souza, G. Teixeira Batista, and L. Bovino Couto. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management* 117:149-167.

Overman, J. P. M., H. J. L. Witte, and J. G. Saldarriaga. 1994. Evaluation of regression models for aboveground biomass determination in Amazon rainforest. *Journal of Tropical Ecology* 10:207-218.

Ovington, J. D., and J. S. Olson. 1970. Biomass and chemical content of El Verde lower montane rain forest plants. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico,* ed. H. T. Odum and R. F. Pigeon, Chapter H 2, 53-77. Washington, D. C.: The University Press of Virginia.

Parresol, B. R. 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. *Forest Science* 45:573-593.

Phillips, O. L., Y. Mahli, N. Higuchi, W. F. Laurance, P. Núñez-Vargas, R. Vásquez-Martinez, S. Laurance, L. V. Ferreira, M. Stern, S. L. Brown, and J. Grace. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439-442.

Phillips, O. L., Y. Malhi, B. Vinceti, T. Baker, S. L. Lewis, N. Higuchi, W. F. Laurance, P. Núñez-Vargas, R. Vásquez-Martinez, S. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 2002. Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications* 12:576-587.

Popper, N., C. Domínguez Cristóbal, A. Santos, N. Méndez Irizarry, E. Torres Morales, A. E. Lugo, Z. Z. Rivera Lugo, B. Soto Toledo, M. Santiago rizarry, I. Loucil Rivera, L. A. Zayaz, and C. Colón. 1999. A comparison of two secondary forests in the coffee zone of central Puerto Rico. *Acta Científica* 13:27-41.

Rivera, L. W., and T. M. Aide. 1998. Forest recovery in the karst region of Puerto Rico. *Forest Ecology and Management* 108:63-75.

Rudel, T. K., M. Perez-Lugo, and H. Zichal. 2000. When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. *Professional Geographer* 52:386-397.

Scatena, F. N., W. L. Silver, T. Siccama, A. Johnson, and M. J. Sanchez. 1993. Biomass and nutrient content of the Bisley Experimental Watershed, Luquillo experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica* 25:15-27.

Schroeder, P., S. Brown, J. Mo, R. A. Birdsey, and C. Cieszewski. 1997. Biomass estimation for temperate broadleaf forests of the United States using inventory data. *Forest Science* 43:424-434.

Silver, W. L., L. M. Kueppers, A. E. Lugo, R. Ostertag, and V. Matzek. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. *Ecological Applications* 14:1115-1127.

Smith, J. E., L. S. Heath, and P. B. Woodbury. 2004. How to estimate forest carbon for large areas from inventory data. *Journal of Forestry* 102:25-31.

Suárez-Rozo, M. d. R., and L. Pérez-Alegría. 2004. A methodology for forest inventory using GIS techniques for carbon sequestration analysis in the Río Grande de Arecibo watershed. In Proceedings of the ASAE/CSAE Annual International Meeting, Ottawa, Ontario, Canada.

Wadsworth, F. H. 1949. The development of the forest lands resources of the Luquillo Mountains, Puerto Rico. PhD. Dissertation. University of Michigan, Ann Arbor, MI.

Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester* 11:38-47.

Weaver, P. L. 1987. Structure and dynamics in the Colorado forest of the Luquillo Mountains, Puerto Rico. PhD. Dissertation. University of Michigan, East Lansing, MI.

Weaver, P. L. 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. *Biotropica* 22:83-89.

Weaver, P. L. 1994. Effects of hurricane Hugo on trees in the Cinnamon Bay watershed, St. John, U.S. Virgin Islands. Caribbean Journal of Science 30:255-261.

Weaver, P. L. 1996. Forest productivity in the Cinnamon Bay watershed, St. John, U.S. Virgin Islands. *Caribbean Journal of Science* 32:89-98.

Weaver, P. L. 1998. Hurricane effects and long-term recovery in a subtropical rain forest. In Forest biodiversity in North, Central and South America and the Caribbean. Research and Monitoring. ed. F. Dallmeier and J. A. Comiskey, Chapter 13, 249-270, Parthenon Publishing Group, Washington, D.C.

Weaver, P. L. 2000. Elfin woodland recovery 30 years after a plane wreck in Puerto Rico's Luquillo mountains. *Caribbean Journal of Science* 36:1-9.

Weaver, P. L., and A. J. Gillespie. 1992. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. *Commonwealth Forestry Review* 71:35-39.

Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing terrestrial productivity. In Primary Productivity of the Biosphere. ed. H. Lieth and R. H. Whittaker, 55-118, Springer-Verlag, New York, NY.