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Diameter growth performance of tree functional groups in Puerto Rican secondary tropical forests

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Abstract

Aim of study: Understanding the factors that control tree growth in successional stands is particularly important for quantifying the carbon sequestration potential and timber yield of secondary tropical forests. Understanding the factors that control tree growth in successional stands is particularly important for quantifying the carbon sequestration potential and timber yield of secondary tropical forests. Yet, the high species diversity of mixed tropical forests, including many uncommon species, hinders the development of species-specific diameter growth models.

Area of study: In these analyses, we grouped 82 species from secondary forests distributed across 93 permanent plots on the island of Puerto Rico.

Material and Methods: Species were classified according to regeneration strategy and adult height into six functional groups. This classification allowed us to develop a robust diameter growth model using growth data collected from 1980-1990. We used mixed linear model regression to analyze tree diameter growth as a function of individual tree characteristics, stand structure, functional group and site factors.

Main results: The proportion of variance in diameter growth explained by the model was 15.1%, ranging from 7.9 to 21.7%. Diameter at breast height, stem density and functional group were the most important predictors of tree growth in Puerto Rican secondary forest. Site factors such as soil and topography failed to predict diameter growth.

Key words: *Caribbean forests; growth model; tropical forest succession; Puerto Rico*.

Introduction

For the last fifty years, humans have converted tropical forested landscapes to a wide variety of uses with unprecedented consequences for biodiversity, climate, and other ecosystem services (Lambin and Geist, 2006). Of the many land-cover changes tropical forests are experiencing, one of most significant to ecosystem service provisioning and human well being is the large increase in the extent of secondary forests. The area of degraded and secondary forests in the tropics was recently estimated at 850 million hectares, and this amount is likely to increase dramatically in the future (ITTO, 2002). These forests provide many of the services attributed to primary forests including regulation of water flow and quality, erosion control, carbon sequestration, and timber and non-timber forest products (Chazdon, 2003; Guariguata and Ostertag, 2001; ITTO, 2002). In spite of their increasing extent, dominance, and prevalence in tropical countries, the processes of tropical forest recovery and succession are not well characterized (Chazdon, 2003).

Understanding the factors that control tree growth in successional stands is particularly important for quantifying the carbon sequestration potential and timber yield of secondary tropical forests (Baker *et al.*, 2003). Tree growth integrates competitive interactions for resources between trees at the stand level (Uriarte *et al.* 2004), and suitability of local environmental conditions for a given tree species (*i.e.*, niche partitioning) (Keddy, 1989; Whittaker, 1975). Teasing apart the importance of local and regional processes in explaining intra- and interspecific variation in tree growth is critical to the development of sustainable management of forest ecosystems, particularly in mixed-species and uneven-aged stands (Canham *et al.*, 2006).

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The island of Puerto Rico has experienced multiple cycles of deforestation and forest recovery in the past two centuries (Lugo *et al.*, 1981). Deforestation in Puerto Rico was rapid during the 19th century, with deforested area peaking in the middle of the 20th century, as sugarcane became the dominant cash crop (Franco *et al.*, 1997). Forest cover reached a low of 6% in the late 1940s and then rose to 32% of the island's area by 1990 (Birdsey and Weaver, 1982), with total forest area increasing from 279,000 hectares in 1980 to 287,000 hectares in 1990 (Franco *et al.*, 1997) and reaching 510,157 ha in 2003 (Brandeis *et al.*, 2007). As a result of these historical processes, the present day Puerto Rican landscape is a fragmented, dynamic mosaic of shifting land uses (Grau *et al.*, 2003). As such, it contains a range of secondary forest patches of different ages, and therefore stand structure and composition, distributed across a number of environmental gradients (Brandeis *et al.*, 2007; Helmer *et al.*, 2008). This landscape provides an unparalleled opportunity to examine the influence of environmental and stand scale level drivers on forest biomass recovery.

The study of tree growth in tropical forests is challenging (Parresol, 1995). These ecosystems can contain a large number of tree species but the majority of them occur at low densities (Terborgh, 1993). Characterization of growth dynamics for the high diversity of species often requires repeated census data from multiple permanent forest plots, a challenging and time consuming task. Even with a large amount of data from multiple plots, the number of observations for uncommon species is often not sufficient for reliable parameter estimation. One solution is to classify tree species into a smaller number of functional groups, thus increasing the size of the sample used for parameter estimation (Gourlet-Fleury *et al.*, 2005). Historically, forest modelers have used a variety of grouping criteria including taxonomic affinity, ecological guilds, similar growth dynamics, and several statistical approaches (see review in Vanclay (1994)). Such groups provide practical and meaningful classifications of tropical forest species, which are needed both by foresters, for modeling growth and yield, and by ecologists, to explain the life history diversity in tropical forest trees. By recognizing groups of species that share suites of covarying characteristics we may be able to scale-up from the well-studied responses of few species, to model community- or stand-level responses to perturbations such as climate change or tree harvesting (Vanclay, 1994). The main purpose of recognizing aggregations of traits in life histories is thus to provide a semi-quantitative foundation for these practical objectives, while in practice most ecologists emphasize continua rather than discontinuities in the spectrum of life histories of coexisting species.

Permanent plot data from National Forest Inventories (NFI) typically cover large geographic areas and provide some of the best coverage of the full range of variability with respect to management treatments, site quality, forest structure, and tree species. Many tree diameter growth models have been fitted using national forest inventory data (Andreassen and Tomter, 2003; Lessard *et al.*, 2001; Monserud and Sterba, 1996; Wykoff, 1990). The sampling methodology of many NFI datasets, however, was not specifically designed to develop growth and yield models and, in some cases, may lead to errors in diameter growth estimates (*e.g.*, Trasobares *et al.*, 2004). By assuming that measurement errors occur randomly in the data, however, the large sample should compensate for this deficiency (Monserud and Sterba, 1996).

In this paper, we use data collected by the US Forest Service Forest Inventory and Analysis Program in 93 permanent plots in Puerto Rico between 1980 and 1990 to examine the diameter growth of functional groups of tropical trees in relation to individual tree, stand and environmental characteristics. To this end, we first classify 1,142 trees from 81 species into 6 functional groups based on regeneration strategy (shade intolerant/shade tolerant dichotomy) and adult height. Second, we use linear mixed model regression to identify individual, stand, functional group and environmental drivers of tree growth.

Materials

Study area

Puerto Rico is a mountainous Caribbean island (latitude range: 17°45'N to 18°30'N; longitude range: 66°15'W to 67°15'W) that stretches 160 km east to west and 55 km north to south. The trade winds approach the island from the northeast and as a result of encountering the mountains create a distinct precipitation gradient with areas in the southwest receiving less than half the annual rainfall (~750 mm) than areas in the northeast (~1,500-2,000 mm). Mean annual temperatures range between 19.4 to 29.7°C with cooler temperatures occurring at higher elevations (Daly *et al.*, 2003). The steep climate gradient, a large elevation range, and a complex geology have generated striking environmental variation within the island. Puerto Rico contains six Holdridge life zones: Subtropical moist forests account for 62% of Puerto Rican forests, subtropical wet forests and rain forest combined covers 23%, subtropical dry forest 14%, and combined subtropical lower montane wet and rain forest slightly over 1% (Ewel and Whitmore, 1973; Holdridge, 1967). Vegetation ranges from dry, semi deciduous forests in patches and bands on the north and east coasts and in the southwest part of the island, to moist forests that cover the major proportion of the island, and wet and rain forests, including cloud forests, at higher elevations (Daly *et al.*, 2003).

Plot data

In 1980, the US Forest Service's Forest Inventory and Analysis (FIA) program and International Institute of Tropical Forestry (IITF) conducted a forest inventory of the Commonwealth of Puerto Rico. This inventory had the primary objective of assessing the timber production potential of the island's forests (Birdsey and Weaver, 1982). The plots were systematically spaced across the island on a 3 × 3 km grid design (900 ha per square). Areas that were excluded from the inventory included public forests, floodplains, urban development, mangrove forests, critical watersheds with high rainfall, dry subtropical life zones, and areas with poorer soils, or steep slopes *(i.e.*, >60%). Permanent plots were installed in 2 of 6 forested Holdridge zones that were considered to have potential for commercial production: subtropical moist and subtropical wet forests. The island's forests were re-surveyed in 1990, re-measuring 93 plots from the 1980 set using the same methodology (Franco *et al.*, 1997).

For each of the 93 plots, we assessed a number of biophysical variables including climate, topography, and soils. Climate variables values were assigned of the nearest weather station from 47 National Weather Service cooperative stations (Daly *et al.*, 2003). Precipitation and elevation were used as drivers under the assumption that cooler temperatures and relatively high precipitation in the higher elevations may accelerate biomass accumulation relative to warmer areas (Daly *et al.*, 2003). However, high levels of precipitation and low temperature can also lead to soil saturation and low physiological activity leading to lower tree growth rates at higher elevation (Silver *et al.*, 1999). Average annual precipitation (mm), was calculated from data collected for the years 1963 to 1995.

Trees may grow faster on slopes facing moisture bearing wind, which in Puerto Rico tend to face north-northeast (Daly *et al.*, 2003; Weaver, 1991). We used 30 × 30 m SRTM elevation data from USGS to calculate aspect. Tree growth may also proceed faster in fertile relative to poor soils. To evaluate the effect of soil fertility on tree growth, we used soil agricultural capacity, a measure of agricultural suitability. Agricultural capacity data group soils into classes according to several criteria including erosion and moisture retention potential, soil depth, and presence of toxic salts, with one being the most fertile and ten being least fertile (USDA, 2007).

Tree data

Growth data used in this study are from 1,142 trees identified and measured in the 93 plots. Each plot contained a 3 point cluster with the points being 25 m apart. Each point consisted of two fixed plot radius tallies where all saplings from 2.5 to 12.5 cm were measured and recorded, and a variable plot tally using a 2.5 m Basal Area Factor (BAF) prism where all "in" trees 12.5 cm and larger were measured and recorded. In addition diameter and crown class (emergent, dominant, co-dominant, intermediate, or overtopped) of all trees were recorded, as well as taxonomic identity and height. For the analyses presented here we used diameter growth increments between the 1980 and 1990 censuses as the response variable. To assess the potential effect of tree competition on tree growth we used the measure of tree basal area in each plot obtained using the BAF prism as well as crown class of the focal tree. Crown class categories were reclassified as upper-canopy (emergent, dominant and co-dominant) and subordinate (intermediate and overtopped) for the analyses.

Methods

Definition of functional groups

Plant functional types (PFTs) are non-phylogenetic groupings of species that show close similarities in their resource use and response to environmental and biotic controls (Wilson, 1999). To classify species into groups or guilds imposes a degree of simplification which reduces information content, but reveals general patterns and facilitates predictions about forest dynamics processes.

For our study, species were grouped on the basis of two criteria: regeneration strategy (shade intolerant/shade tolerant dichotomy) and adult height, defined as average maximum tree height (Baker *et al.*, 2003; Kariuki *et al.*, 2006; Swaine and Whitmore, 1988). Shade intolerants (*I*) are species whose seeds can only germinate in open canopy gaps while shade tolerant species (*T*) are those that can germinate and grow in the shade. Species were further classified using adult height as a criterion into small (*S*) (<10 m), medium (*M*) (10-25 m) and large (*L*) (>25 m) classes. Adult height represents the vertical space occupied by the adult, an ecologically meaningful metric (Alder, 1995). Classification along these two axes resulted in 6 groups (Tables 1 & 2). Data on regeneration strategy and adult height were obtained from the Natural Resources Conservation Service (USDA, 2010b), Forest Service (USDA, 2010a), and Little and Wadsworth (1964). We then used ANOVA to identify whether these groups exhibited different mean growth.

Diameter growth model

Our growth model assumes that each species has a maximum potential growth rate, which is adjusted to account for (1) the characteristics of the focal individual tree; (2) the structure and composition of the stand, including potential metrics of stand development and competition between trees; (3) functional group; and (4) habitat (site) variables. Using this rationale, we divided explanatory variables into five groups:

1. Single-tree variables: diameter at breast height (*d,* cm), height (*h,* m), and crown class of the focal tree (upper-canopy or subordinate).
2. Stand variables: mean diameter (D_m, cm), density (*N*, trees/ha), and basal area (*BA,* m²/ha).
3. Single tree competition: basal area of all trees larger than the focal tree within the plot (*BAL,* m²/ha), and the relation of diameter at breast height and mean squared diameter (d / D_m^2, cm^{-1}).
4. Functional group: large shade tolerants (*LT*), large shade intolerants (*LI*), medium shade tolerants (*MT*), medium shade intolerants (*MI*), small shade tolerants (*ST*), and small shade intolerants (*SI*).
5. Site variables: elevation (m), aspect (%), mean annual rainfall (mm), and soil fertility class.

Different forms of diameter growth were considered for the dependent variable: diameter increment ($D_2 - D_1$), 10-year diameter growth rate ($D_{rate} = [(D_2 - D_1) / D_1)]$ and square diameter increment ($D_2^2 - D_1^2$). We log transformed diameter growth with three objectives: i) to make the error variances more nearly homogeneous; ii) to improve additivity; iii) to produce a more nearly normal error distribution (Finney, 1989). Since the dependent variable is transformed prior to estimation, there is an inherent negative bias in the method. To account for this bias, we applied the empirical bias corrector $\frac{id_{10}}{\exp\left[\ln \widehat{id}_{10}\right]}$ suggested by Snowdon (1991), where id_{10} is the mean of measured diameter increments for ten year period ($d_2 - d_1$) and $\widehat{id}_{10}$ is the mean of estimated diameter increments. To obtain normally distributed residuals with constant variance and to address the existence of negative or zero growth, we added 1 to each growth observation before applying the logarithm transformation (Hökkä *et al.*, 1997).

We fitted a mixed linear regression model to the diameter growth data using the covariates describe above (Laird and Ware, 1982). Plot was included in the analysis as a random effect added to the intercept parameter. Models parameters were estimated using REML to derive unbiased estimates of the variance and covariance parameters associated with random effects. Independent variables to be included in the function were selected through visual analysis of data plots versus explanatory variables and a backward selection procedure. The most appropriate model was determined from residual analyses, Akaike information criterion (*AIC*), and coefficient of determination (R^2) values. All analyses were conducted using R statistical software (R Development Core Team, 2009).

Results

We classified 81 species into six functional groups using regeneration strategy and adult height (Table 2). As expected, average diameter growth for shade tolerant groups (*LT*, *MT*, and *ST*) was lower than for

Table 1. Functional groups defined on the basis of regeneration strategy and adult height of the species. Family is provided in parenthesis

Large shade tolerant species (*LT*)

Dacryodes excelsa (Bursereaceae)
Hymenaea courbaril (Fabaceae)
Manilkara bidentata (Sapotaceae)
Micropholis guyanensis (Sapotaceae)

Large shade intolerant species (*LI*)

Andira inermis (Fabaceae)
Cinnamomum elongatum (Lauraceae)
Guarea guidonia (Meliaeceae)
Homalium racemosum (Flacourtiaceae)
Nectandra turbacensis (Lauraceae)
Sloanea berteriana (Elaeocaopaceae)
Spathodea campanulata (Bignoniaceae)
Zanthoxylum martinicense (Rutaceae)

Medium shade tolerant species (*MT*)

Bucida buceras (Combretaceae)
Casearia guianensis (Flacourtiaceae)
Clusia rosea (Clusiaceae)
Inga laurina (Fabaceae)
Magnolia portoricensis (Magnoliaceae)
Neolaugeria resinosa (Rubiaceae)
Ocotea leucoxylon (Lauraceae)
Ormosia krugii (Fabaceae)
Persea americana (Lauraceae)
Prestoea acuminata var. Montana (Arecaceae)
Roystonea borinqueña (Arecaceae)
Terminalia catappa (Combretaceae)
Thespesia grandiflora (Malvaceae)

Medium shade intolerant species (*MI*)

Alchornea latifolia (Euphorbiaceae)
Artocarpus altilis (Moraceae)
Buchenavia tetraphylla (Combretaceae)
Bursera simaruba (Burseraceae)
Byrsonima spicata (Malpighiaceae)
Calophyllum antillanum (Clusiaceae)
Cecropia schreberiana (Cecropiaceae)
Cedrela odorata (Meliaceae)
Cordia alliodora (Boraginaceae)
Cupania americana (Sapindaceae)
Dendropanax arboreus (Araliaceae)
Erythrina poeppigiana (Fabaceae)
Exothea paniculata (Sapindaceae)
Ficus citrifolia (Moraceae)
Guazuma ulmifolia (Sterculiaceae)
Inga vera (Fabaceae)
Lonchocarpus heptaphyllus (Fabaceae)
Mammea americana (Clusiaceae)
Mangifera indica (Anacardiaceae)
Palicourea croceoides (Rubiaceae)
Petitia domingensis (Verbenaceae)
Schefflera morototonii (Araliaceae)
Spondias dulcis (Anacardiaceae)
Spondias mombin (Anacardiaceae)
Tabebuia heterophylla (Bignoniaceae)
Trichilia pallida (Meliaceae)
Vitex divaricata (Verbenaceae)

Small shade tolerant species (*ST*)

Casearia sylvestris (Flacourtiaceae)
Citrus × paradisi (Rutaceae)
Citrus × sinensis (Rutaceae)
Coccoloba diversifolia (Polygonaceae)
Coffea liberica (Rubiaceae)
Eugenia montícola (Myrtaceae)
Guarea glabra (Meliaceae)
Myrcia deflexa (Myrtaceae)
Myrsine cubana (Myrsinaceae)
Pouteria multiflora (Sapotaceae)
Psidium amplexicaule (Myrtaceae)
Psidium guajava (Myrataceae)
Sagraea umbrosa (Melatomataceae)
Syzygium jambos (Myrtaceae)

Small shade intolerant species (*SI*)

Annona squamosa (Annonaceae)
Casearia arborea (Flacourtiaceae)
Casearia decandra (Flacourtiaceae)
Castilla elastica (Moraceae)
Cordia sulcata (Boraginaceae)
Cyathea arborea (Cyatheaceae)
Guettarda scabra (Rubiaceae)
Gyminda latifolia (Celastraceae)
Gymnanthes lucida (Euphorbiaceae)
Meliosma herbertii (Sabiaceae)
Miconia impetiolaris (Melastomataceae)
Miconia prasina (Melastomataceae)
Myrcia splendens (Myrtaceae)
Sideroxylon salicifolium (Sapotaceae)
Tetrazygia elaeagnoides (Melastomataceae)
Turpinia occidentalis (Staphyleaceae)

Table 2. Sample sizes and mean values for single-tree, stand-level, and site covariates included in the model for the six functional groups indentified. Standard deviation is provided in parentheses

Species group	LT	LI	MT	MI	ST	SI
No. of trees	29	255	161	444	141	112
No. of plots	7	64	54	85	46	42
Single-tree size variables						
d_1	22.0	26.4	19.68	29.49	12.05	10.13
(cm)	(10.6)	(17.7)	(13.4)	(21.9)	(13.2)	(10.9)
Growth (d_2-d_1)	3.9	5.8	2.29	4.38	1.6	1.44
(cm)	(3.2)	(5.8)	(2.7)	(5.0)	(2.1)	(2.1)
Stand variables at 1980						
N	949.0	674.86	992.81	699.83	939.55	1267.94
(stems/ha)	(688.3)	(387.7)	(662.0)	(519.3)	(580.6)	(848.5)
D_m	23.8	25.86	20.78	25.08	18.95	14.91
(cm)	(6.0)	(8.9)	(8.7)	(10.6)	(10.2)	(8.3)
BA	17.79	15.71	17.37	15.95	15.69	11.81
(m^2/ha)	(8.8)	(12.8)	(11.6)	(14.1)	(14.2)	(8.7)
Competition variable at 1980						
BAL	8.56	7.20	8.8	6.11	10.33	7.73
(m^2/ha)	(8.3)	(9.6)	(10.6)	(8.4)	(11.1)	(8.1)
Site variables						
Elevation	627.59	407.81	470.78	397.22	443.69	410.54
(m)	(258.1)	(223.9)	(247.7)	(248.6)	(241.6)	(260.3)
Aspect	192.30	195.54	181.0	191.72	197.53	190.16
(degrees)	(130.4)	(103.9)	(111.8)	(101.9)	(98.7)	(101.4)
Mean annual precipitation	2099.38	1940.75	2019.45	1964.91	1948.01	1948.75
(mm)	(135.8)	(241.8)	(245.5)	(248.6)	(165.9)	(231.5)

LT: large shade tolerants; LI: large shade intolerants; MT: medium shade tolerants; MI: medium shade intolerants, ST: small shade tolerants; SI: small shade intolerants.
d_1: diameter at breast height at 1980; d_2: diameter at breast height at 1990; N: density; D_m: mean diameter; BA: basal area; BAL: basal area of trees larger than subject tree.

shade intolerant groups (*LI*, *MI* and *SI*, respectively). Average growth rates for large species (*LT* and *LI*) were also higher than for medium (*MT* and *MI*) and small ones (*ST* and *SI*). Fig. 1 shows overlapped intervals between groups, so an ANOVA test was carried out to evaluate the differences between the means (Fig. 2). No difference was found between shade intolerant and tolerant small trees, and shade intolerant large and tolerant medium trees. Eventually, the mixed model considered four different groups: shade intolerant large group (*LI*), shade tolerant large and shade intolerant medium group (*LTMI*), shade tolerant medium group (*MT*) and small group (*S*). However, these average growth rates could potentially gloss over important differences in the composition, stand structure, and location of the 93 stands used in the analyses.

After considering different forms of diameter growth, the logarithm of tree diameter growth $[ln(D_2 - D_1 + 1)]$ was chosen as the dependent variable for the response model. Diameter growth data was fitted to individual tree, stand, functional group and site covariates using a mixed linear model. The fixed parameter estimates were logical and significant at the 0.01 level. The random parameter estimate of the plot factor was significant at the 0.01 level. The empirical ratio estimator suggested by Snowdon (1991) for all data was 2.819618018. The expression of the individual-tree diameter growth model was:

$$
\begin{aligned}
&\ln\left[\left(d_{ij2}-d_{ij1}\right)+1\right]=0.4828\left(0.0485\right)\\
&+0.086\left(0.0119\right)\cdot ln(d_{ij1})-0.000098\left(0.00003\right)\cdot N_j\\
&-0.0859\left(0.0269\right)\cdot LTMI-0.2179\left(0.0356\right)\cdot MT\\
&-0.2464\left(0.0337\right)\cdot S+u_j+\varepsilon_{ij}\\
&u_j\sim N\left(0,\ 0.0957\right)\\
&\varepsilon_{ij}\sim N\left(0,\ 0.3239\right)
\end{aligned}
$$

where: d_{ij2} = breast height diameter (cm) over the following ten years, 1990 on our data set, belong to the observation i taken in the j plot,; d_{ij1} = present, 1980 in our data set, breast height diameter (cm) belong to the observation i taken in the j plot (cm); N_j = present density in the j plot (trees/ha); *LTMI* = Factor whose value is 1 if the observation belongs to the shade tolerant large or shade intolerant medium group and 0 if not; *MT* = Factor whose value is 1 if the observation belongs to the tolerant medium group and 0 if not; *S* = Factor whose value is 1 if the observation belongs to the small size group and 0 if not; u_j is a random plot parameter specific to the observations taken in the j plot: and ε_{ij} are residual error terms. In brackets the standard error of the parameter is shown.

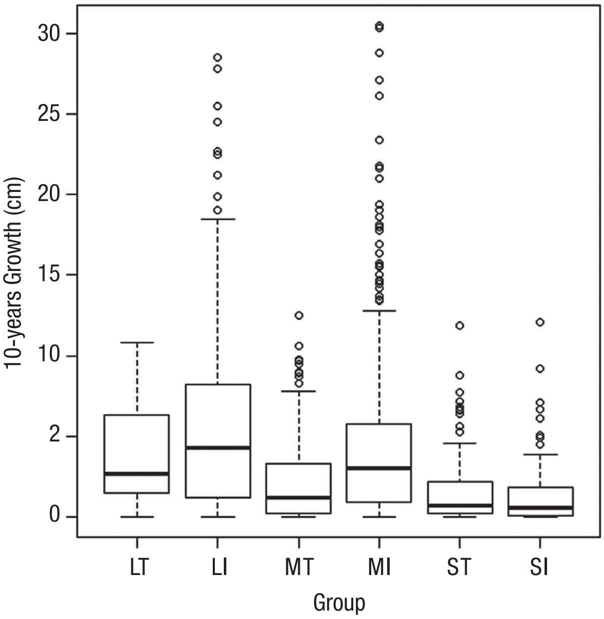

Figure 1. Means, first and third quartile in diameter growth over 10-years for the six functional groups included in the study (*LT*, Large shade tolerant species; *LI*, Large shade intolerant; *MT*, medium shade tolerant; *MI*, medium shade intolerant, *ST*, small shade tolerant; *SI*, small shade intolerant).

Overall, observed values reached more extreme values than predicted values, but average predictions matched observed data (Fig. 3). Examination of residuals identified no discernible trends, so the assumption of normal and independent distribution was validated. The proportion of variance explained

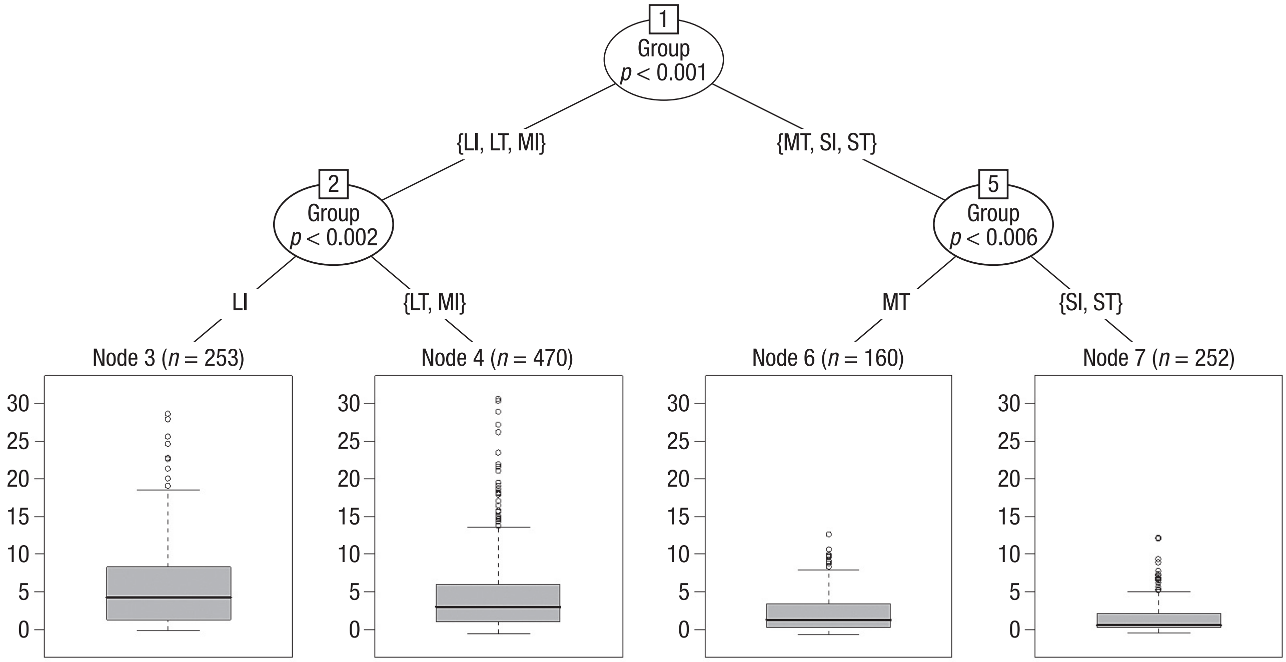

Figure 2. An ANOVA tree for the species groups.

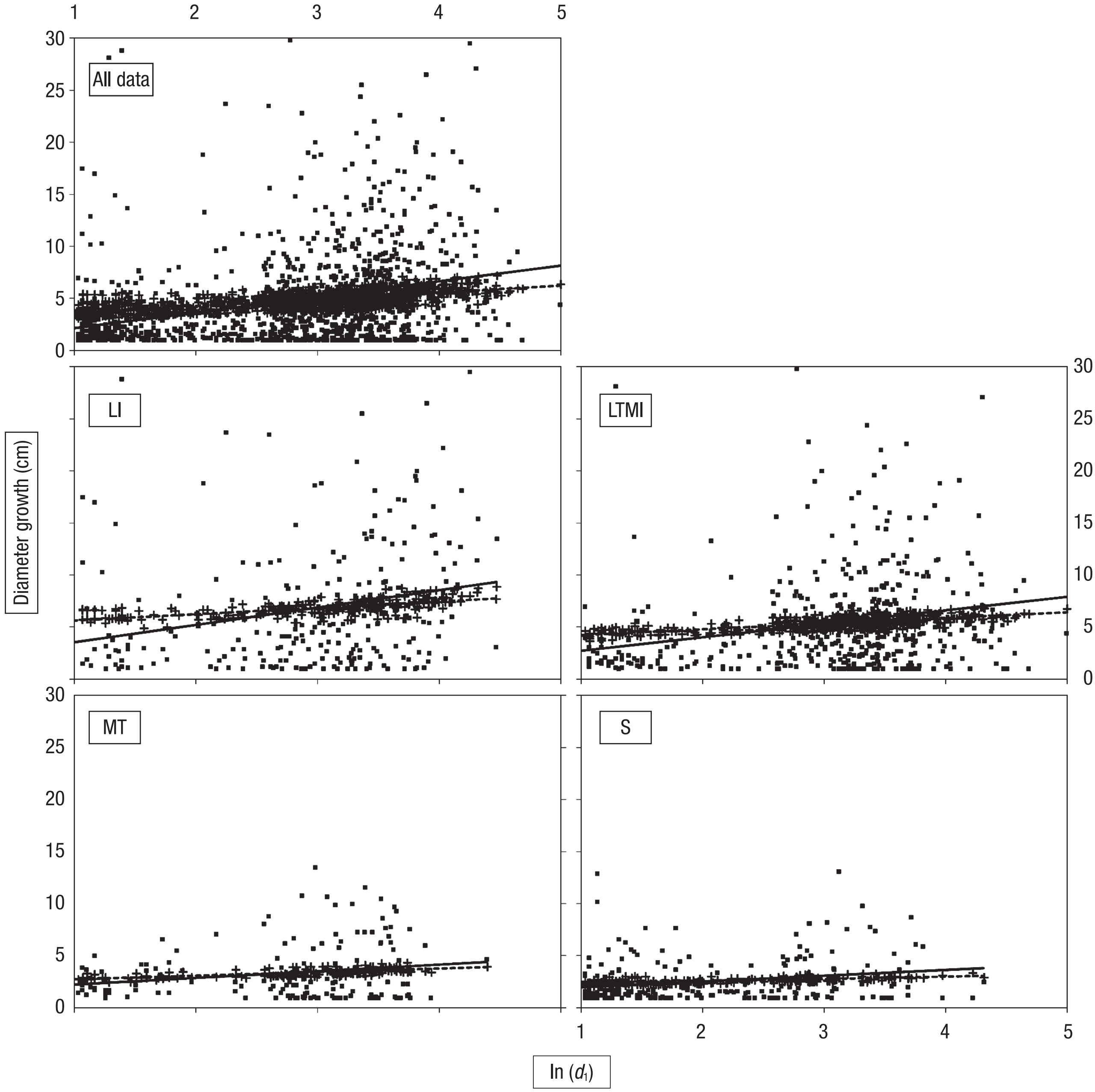

Figure 3. Comparison between observed and predicted, including plot's EBLUPs, tree diameter growth for all groups (*LI*, Large shade intolerant species; *LTMI*, large shade tolerant and medium shade intolerant; *MT*, medium shade tolerant; *S*, small species). Predicted values are indicated with cross dots and dashed lines and observed data with square dots and solid lines.

by the model considering all data was 18.8%, ranged from 8.8% for the large shade tolerant and medium shade intolerant group to 74.1% for small species. Snowdon's ratios calculated separately for each group were all positive and were taken into account to correct the biased results given by logarithmic regressions (Snowdon, 1991) (Table 3).

Of the individual tree variables, size was the most significant predictor of growth. The shape of the relationship between diameter at breast height (d_1) and diameter growth have the skewed unimodal form that is typical of tree growth processes. The majority of the diameters were less than 50 cm (1043 trees out of 1135 trees), so the data set is still on the positive relation

Table 3. Snowdon ratio and R^2 explained by the growth model for the four functional groups identified in Puerto Rico. Groups include shade intolerant large group (*LI*), shade tolerant large and shade intolerant medium group (*LTMI*), shade tolerant medium group (*MT*) and small group (*S*)

Functional group	LI	LTMI	MT	S	All
Snowdon ratio	3.46	2.99	2.22	1.86	2.82
***R^2* explained**	0.133	0.088	0.508	0.741	0.188

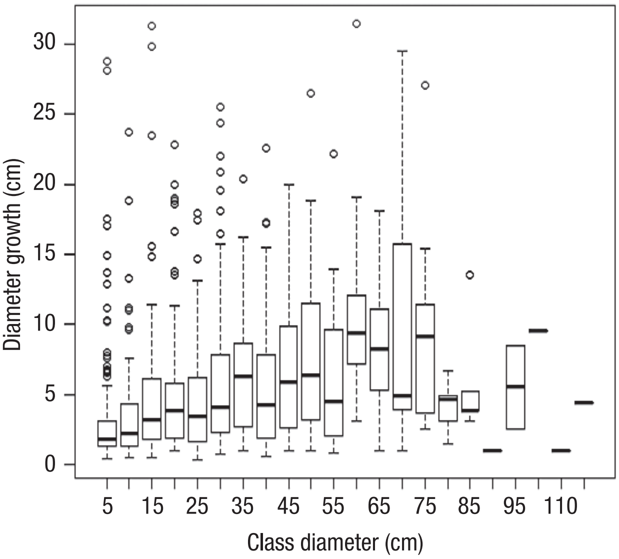

Figure 4. Relationship between initial class diameter and diameter growth over 10-years for all data.

area of the skewed unimodal form (Fig. 4). This is shown in the model where diameter growth increased with size. Surprisingly, height was not a significant predictor of diameter growth, possibly because of the high correlations between diameter and height (Brandeis *et al.*, 2009).

Density (*N*) had a negative effect on diameter growth. This result confirms that an increase in competition leads to a reduction in the diameter growth.

The functional groups indicate higher growth for large species relative to medium and small species. Except small size species, intolerant species show a higher growth versus tolerant species as well.

We included a number of site quality variables in our analyses. In contrast to the important effects of individual tree, stand level variables and functional group, none of the site variables were significant predictors of growth.

Discussion

We classified 81 species from 1,142 individuals distributed across 93 permanent plots into fourfunctional groups based on regeneration strategy and adult height. Our goal was to use this classification to explain variation in diameter growth across successional stands. Average annual diameter increment for these species was 0.37 cm, ranging from about 0.01 cm for *Persea americana* to 0.92 cm in *Spathodea campanulata*. These growth rates are comparable to those found in other studies (Brandeis, 2009; Weaver, 1979). Further sampling is needed to provide data for a wider range of species with potentially differing growth forms and to provide further insight of tropical forest dynamics in Puerto Rico.

Tree growth rates in our study decreased from shade intolerant and canopy emergent species through shade tolerant and middle and low story late successional species, as others results in literature (Francis and Lowe, 2000; Kariuki *et al.*, 2006), supporting the notion that interspecific variation in maximum potential growth rate is one of the most important factors in the definition of functional groups (Baker *et al.*, 2003). Variability in diameter increments between functional groups was considerable, with the mean value of the median 10-year diameter increment almost 4 times greater in fastest growing group (Large shade intolerant) relative to the slowest (Small shade intolerant).

We use mixed model regression to identify individual, stand, functional group and environmental drivers that could account for variation in tree growth. The explained variance obtained (R^2 = 18.8%, ranged from 8.8% to 74.1%) is comparable to others tropical growth models. Parresol (1995) fitted three equations to growth data for 15 species in a moist tropical forest in Puerto Rico, accounting for 12% to 69% of variance of growth. In a lowland evergreen rain forest in French Guiana, Gourlet-Fleury and Houllier (2000) built 15 groups from 87 species to develop a diameter increment model, and extended it to 173 species, obtaining a pseudo-R^2 between 0.07 and 0.43. Similar results were obtained by Vanclay (1991) in Queensland (R^2 = 0.45) and Chai and LeMay (1993) in Sarawak (R^2 = 0.07-0.45). Across all studies a large percentage of growth increment remains unexplained. Possible sources for this variation include physical measurement error (Prodan, 1965); (Monserud and Sterba, 1996), pure error (Draper and Smith, 1998) and failure to include variables that influence tree growth in the model, as genetic or climatic factors. The last class is of greatest importance for models of tropical forest dynamics (Uriarte *et al.*, 2004). Another possible source of variation is the inherent relation among random plot effects and functional groups, since not all the functional groups are present in all the plots.

Many variables used in plantation growth models have little relevance in tropic rainforests (*e.g.*, age, top height, mean diameter), since growth must be predicted from accessible variables such as diameter and stand basal area (Vanclay *et al.*, 1995). If trees were all of the same age and size (diameter and height), diameter growth is an adequate measure of tree growth and results can be compared across the board. This is done in plantation forestry. Our study is an improvement because by classifying species by functional groups, we reduce the variation in tree size and thus differences in diameter growth appear.

The positive logarithmic relationship between diameter at breast height (d) and diameter growth suggests that data represent young stands and where trees have not reached the maximum growth rate yet. Once large trees reach maximum size growth rapidly approaches zero.

To account for the effects of stand structure on diameter growth we considered a number of indicators of competition, including dominance class, mean diameter of the stand, stem density and basal area. The negative effect of stem density on diameter growth confirms that in general, stand-level competition leads to a reduction in diameter growth (Gourlet-Fleury and Houllier, 2000).

Large species group shows higher growth than medium and small species. Irradiance declines exponentially with decreasing height in tropical forests (Yoda, 1978) and increased canopy illumination has a clear, positive effect on tree growth, not a surprising result since irradiance plays a prominent role in determining the carbon acquisition potential of forest plants (Lüttge, 2008). Lower growth for the tolerant species groups implies that the diameter growth rate of intolerant species groups is higher. In a study of 15 species in tropical forest in Puerto Rico, Parresol (1995) demonstrated that maximum growth rates were five times higher in upper-canopy trees than in trees in the subordinate crown class categories.

We also considered a number of site covariates in our analyses including precipitation, elevation, aspect, and soil fertility class. Habitat characteristics influence soil water availability, solar radiation, and probably soil nutrient availability, factors that have been shown to influence stand-level growth responses (Kariuki *et al.*, 2006). Surprisingly, the relationship between relative diameter growth and site characteristics was not statistically significant. Similar attempts to incorporate site information in diameter growth models of tropical forest have encountered mixed success. For instance, Gourlet-Fleury and Houllier (2000) found negligible effects of topographical and soil factors for modeling diameter increment in a lowland evergreen rain forest in French Guiana. Clark *et al.* (1998), working in forest in an aseasonal climate in Costa Rica with adults of nine canopy or emergent tree species, found no difference in growth rate between two well-drained soil-types that differed in available P concentration by a factor of two. In addition, Ashton and Hall (1992) found no correlation between the proportional diameter growth (1965-1985) of large trees (dbh >30 cm), and soil nutrient status across 13 plots in high-rainfall forests in Borneo. In contrast, Weaver (1979) linked moisture stress, saturated soils and reduced solar radiation to changes of the growth in Puerto Rican forest trees. The absence of site effects may in part be the result of the way in which site characteristics are measured. For instance, climate data are typically collected at the nearest weather station to the plot, and may fail to capture important microsite characteristics. Another potential reason is that site characteristics are confounded with the range of observed tree sizes and stand characteristics, hindering our ability to detect site effects.

This study demonstrates that using tree functional group classifications based on regeneration strategy and adult height can improved relatively efficient models. Tree diameter and adult height were the most important predictors of tree growth in Puerto Rican secondary forest, followed by density and regeneration strategy. The effects of stand-level covariates were less consistent while soil and topography failed to predict diameter growth for the majority of tree species. Tree diameter growth can vary widely between measurements periods over the short term (Clark and Clark, 1994), and is partly due to variation in growth conditions, which are captured to a certain extent in this study. Moreover, using these diameter growth models to estimate changes in tree volume must be done with caution because some of the fit statistics may be strongly biased (Hasenauer and Monserud, 1997). In sum, the results presented here must be considered as preliminary because they represent a single measurement period (1980-1990), providing only a snapshot of forest dynamics. This work should be seen as part of an ongoing process, and the equations presented here will be refined as additional data becomes available.

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References

Alder D, 1995. Growth modelling for mixed tropical forests. Oxford Forestry Institute, Oxford, UK.

Andreassen K, Tomter SM, 2003. Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. For. Ecol. Manage. 180: 11-24.

Ashton PS, Hall P, 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. Journal of Ecology 80: 459-481.

Baker TR, Swaine MD, Burslem DFRP, 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspectives in Plant Ecology, Evolution and Systematics 6: 21-36.

Birdsey RA, Weaver PL, 1982. The forests resources of Puerto Rico. Resour. Bull. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA, p. 59.

Brandeis TJ, 2009. Diameter Growth of Subtropical Trees in Puerto Rico. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, p. 44.

Brandeis TJ, Helmer EH, Oswalt SN, 2007. The Status of Puerto Rico's Forests, 2003. USDA Forest Service Southern Research Station, Asheville, NC, USA, p. 75.

Brandeis TJ, Randolph KC, Strub MR, 2009. Modeling Caribbean tree stem diameters from tree height and crown width measurements. Mathematical and Computational Forestry & Natural-Resource Sciences 1: 78-95.

Canham C, Papaik MJ, Uriarte M, McWilliams WH, Jenkins JC, Twery MJ, 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecological applications 16: 540-554.

Chai FYC, LeMay VM, 1993. Development and testing of diameter increment models for mixed swamp forests of Sarawak. For. Ecol. Manage. 58: 51-64.

Chazdon RL, 2003. Tropical forest recovery: legacies of human intervention and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6: 51-71.

Clark DA, Clark DB, 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. Journal of Ecology 82: 865-872.

Clark DB, Clark DA, Read JM, 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. Journal of Ecology 86: 101-112.

Daly C, Helmer EH, Quiñones AM, 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. International Journal of Climatology 23: 1359-1381.

Draper NR, Smith H, 1998. Applied Regression Analysis. Wiley-Interscience, New York.

Ewel JJ, Whitmore JL, 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Institute of Tropical Forestry, Río Piedras, Puerto Rico, p. 72.

Finney DJ, 1989. Was this in your statistical text book? V. Transformation of data. Experimental Agriculture 25: 165-175.

Francis JK, Lowe CA, 2000. Bioecología de arboles nativos y exoticos de Puerto Rico y las Indias Occidentales. United States Department of Agriculture, Forest Service. International Institute of Tropical Forestry, Ríos Piedras, Puerto Rico.

Franco PA, Weaver PL, Eggen-McIntosh S, 1997. Forest resources of Puerto Rico, 1990. Southern Resource Bulletin. USDA Forest Service Southern Research Station, Asheville, North Carolina, USA.

Gourlet-Fleury S, Blanc L, Picard N, Sist P, Dick J, Nasi R, Swaine MD, Forni E, 2005. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. Ann. For. Sci. 62: 785-796.

Gourlet-Fleury S, Houllier F, 2000. Modelling diameter increment in a lowland evergreen rain forest in French Guiana. For. Ecol. Manage. 131: 269-289.

Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer E, Zou X, 2003. The ecological consequences of socioeconomic and land-use changes in postagricultural Puerto Rico. Bioscience 53: 1159-1168.

Guariguata MR, Ostertag R, 2001. Neotropical secondary succession: changes in structural and functional characteristics. For. Ecol. Manage. 148: 185-206.

Hasenauer H, Monserud RA, 1997. Biased prediction for tree height increment models developed from smoothed "data". Ecol. model. 98: 13-22.

Helmer EH, Brandeis TJ, Lugo AE, Kennaway T, 2008. Factors influencing spatial pattern in tropical forest clearance and stand age: implications for carbon storage and species diversity. J Geophys Res 113: 165-183.

Hökkä H, Alenius V, Penttilä T, 1997. Individual-tree basal area growth models for scots pine, pubescens birch and norway spruce on drained peatlands in Finland. Silva Fenn. 31: 161-178.

Holdridge LR, 1967. Life zone ecology. Revised. Tropical Science Center, San José, Costa Rica.

ITTO, 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. ITTO in collaboration with CIFOR, FAO, IUCN and WWF, Yokohama, Japan.

Kariuki M, Rolfe M, Smith RGB, Vanclay J, Kooyman RM, 2006. Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. For. Ecol. Manage. 225: 1-14.

Keddy PA, 1989. Competition. Chapman and Hall, London, UK.

Laird NM, Ware JH, 1982. Random-effects models for longitudinal data. Biometrics 38: 963-974.

Lambin EF, Geist H, 2006. Land-use and land-cover change: local processes and global impacts, Berlin, Heidelberg, GE.

Lessard VC, McRoberts RE, Holdaway MR, 2001. Diameter growth models using Minnesota Forest Inventory and analysis data. For. Sci. 47: 301-310.

Little EL, Wadsworth FH, 1964. Common trees of Puerto Rico and the Virgin Islands. U.S. Department of Agriculture Forest Service, Washington, D.C., USA.

Lüttge U, 2008. Physiological ecology of tropical plants. Second edition. Springer-Verlag, Berlin, Heidelberg, Germany.

Lugo AE, Schmidt R, Brown S, 1981. Tropical forests in the Caribbean. Ambio 10: 318-324.

Monserud RA, Sterba H, 1996. A basal area increment model for individual trees growing in even- and uneven-aged forests stands in Austria. For. Ecol. Manage. 80: 57-80.

Parresol BR, 1995. Basal area growth for 15 tropical trees species in Puerto Rico. For. Ecol. Manage. 73: 211-219.

Prodan M, 1965. Holzmesslehre. J.D.Sauerlander, Frankfurt, Germany.

R Development Core Team, 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria.

Silver WL, Lugo AE, Keller M, 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry, 301-328.

Snowdon P, 1991. A ratio estimator for bias correction in logarithmic regressions. Can. J. For. Res. 21: 720-724.

Swaine MD, Whitmore TC, 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75: 81-86.

Terborgh J, 1993. Lebensraum Regenwald-Zentrum biologischer Vielfalt. Spektrum Akademischer Verlag, Heidelberg, Germany.

Trasobares A, Pukkala T, Miina J, 2004. Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain. Ann. For. Sci. 61: 9-24.

Uriarte M, Canham C, Thompson J, Zimmerman JK, 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs 74: 591-614.

USDA, Forest Service, 2010a. www.Treesearch.fs.fed.us. U.S. Forest Service. P.O. Box 96090, Washington, D.C. 20090-6090.

USDA, NRCS, 2007. In, National Soil Survey Handbook, title 430-VI Part 622.

USDA, NRCS, 2010b. The PLANTS Database (http://plants.usda.gov, 7 April 2010). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Vanclay JK, 1991. Aggregating tree species to develop diameter increment equations for tropical rainforest. For. Ecol. Manage. 42: 143-168.

Vanclay JK, 1994. Modelling Forest Growth and Yield - Application to Mixed Tropical Forests. CAB Internat., UK.

Vanclay JK, Skovsgaard JP, Pilegaard Hansen C, 1995. Assesing the quality of permanent sample plot databases for growth modelling in forest plantations. For. Ecol. Manage. 71: 177-186.

Weaver PL, 1979. Tree growth in several tropical forests in Puerto Rico. U.S. Department of Agriculture Forest Service, Sourthern Forest Experiment Station, Nashville, NC, USA, p. 20.

Weaver PL, 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. Interciencia 16: 142-151.

Whittaker RH, 1975. Communities and Ecosystems. 2nd ed., New York, USA.

Wilson JB, 1999. Guilds, functional types and ecological groups. Oikos 86: 507-522.

Wykoff WR, 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36: 1077-1104.

Yoda K, 1978. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. Malaysian Nature Journal 30: 161-177.