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Mapping land cover and estimating forest structure using satellite imagery and coarse resolution lidar in the Virgin Islands

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Abstract

Current information on land cover, forest type and forest structure for the Virgin Islands is critical to land managers and researchers for accurate forest inventory and ecological monitoring. In this study, we use cloud free image mosaics of panchromatic sharpened Landsat ETM+ images and decision tree classification software to map land cover and forest type for the Virgin Islands, illustrating a low cost, repeatable mapping approach. Also, we test if coarse-resolution discrete lidar data that are often collected in conjunction with digital orthophotos are useful for mapping forest structural attributes. This approach addresses the factors that affect vegetation distribution and structure by testing if environmental variables can improve regression models of forest height and biomass derived from lidar data. The overall accuracy of the 29 forest and non-forest classes is 72%, while most the forest types are classified with greater than 70% accuracy. Due to the large point spacing of this lidar dataset, it is most appropriate for height measurements of dominant and co-dominant trees ($R^2 = 72\%$) due to its inability to accurately represent forest understory. Above ground biomass per hectare is estimated by its direct relationship with plot canopy height ($R^2 = 0.72\%$).

Keywords: Land cover, decision tree software, discrete lidar, forest structure, regression modeling, Virgin Islands.

1 INTRODUCTION

Information on land cover, forest type and forest structure for the Virgin Islands is limited to maps of ecological zones and photo interpreted land cover [1,2] and relatively few forest inventory plots. The lack of current land cover data and robust techniques for updating that data, and the sparseness of forest inventory plots relative to the number of different forest types, pose challenges to land managers and researchers in ecologically vulnerable subtropical environments. These challenges are made more acute in Caribbean environments, because the interaction between trade winds and steep topographic gradients cause forest types to change over short distances [3] and high rates of disturbance lead to variable forest structure. In this study, datasets of land cover and forest type are derived from satellite imagery with decision tree software, illustrating a low cost, repeatable approach for creating

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such data. Although decision tree classification is becoming common in remote sensing, only a few studies use decision trees for detailed forest mapping of subtropical islands [4-6].

This study also addresses the characterization of forest structure with airborne light detection and ranging (lidar) when inventory data are sparse. Lidar adds a third (z) dimension to the spatial description of forest types with accurate estimates of vegetation height and above ground biomass [7]. No prior research has addressed the quantification of lidar derived forest structure in the Virgin Islands. Data describing indices of forest structure such as height and biomass can provide important information such as indicators of forest age, species richness and habitat.

Forest distribution and structure in the Virgin Islands has been modified for hundreds of years by both natural and human caused disturbances, including hurricanes and human exploitation. Prior to European colonization, indigenous peoples such as the Carib first cleared forest for food, shelter, and boat building materials. In the 1600 and 1700's Danish and British settlers arrived and began converting forest to intensive agriculture that included coffee, sugar cane and tobacco [8,9,10,11]. As a result, most old growth forest was cleared and has recovered as fragmented secondary forests after the gradual abandonment of agriculture through to the early twentieth century. The forest clearing had lasting impacts on forest structure, ecosystem function and species composition, including the introduction and extinction of exotic and endemic species [12].

Increased pressure from urban development has led to additional forest clearing in the Lesser Antilles [5] and Puerto Rico. The spatial pattern of forest clearing is often influenced by proximity to existing urban areas, roads and topography [13,4]. Islands such as St. Thomas [14] and Tortola have also experienced urban growth at the expense of forested areas over the last decade. About 65% of St. John is protected by the US Park Service including much of its semi-deciduous (including semi-evergreen) and deciduous forests. However, the unprotected low elevation dry forests on that and other islands, which have been shown to be important habitat for many avian species, are considered endangered and susceptible to increasing developmental pressures [15].

The overall goal of this study is to develop an approach for characterizing the structure of varied subtropical island forest formations when available inventory data are relatively sparse. To accomplish this goal, we developed three main objectives. The first objective is to test an improvement to a previously developed approach for using Landsat image mosaics to map land-cover and forest types in persistently cloudy, complex tropical landscapes with decision tree classification software [4-6,16,17]. The improvement is that we use panchromatic-sharpened image mosaics to increase spatial resolution in the resulting maps. We also test whether the approach is applicable to a large area, the Virgin Islands, which includes many islands. The second objective is to test if the coarse-resolution (shot spacing of 2.76m) discrete lidar data that are often collected in conjunction with digital orthophotos are useful for mapping forest structural attributes, including height and biomass, over the steep environmental gradients present on the islands of St. John and St. Thomas. Also, this study tests whether integrating Landsat ETM+ satellite imagery and environmental variables with the lidar data can improve models of forest structural attributes. Whether the large point spacing of such coarse resolution lidar will be adequate to accurately sample and model forest structure parameters has not been tested. Also unknown is whether the range of physiognomic types found across these islands will complicate the estimates of forest height and biomass. Several studies have shown that large footprint scanning lidar accurately predicts forest structure, including canopy height, basal area and above ground biomass in

Douglas fir/western hemlock forests [18,19]. Other studies accurately model forest metrics with discrete lidar, focusing on small tracts of homogeneous forest stands and small foot-print sensors [20]. Accurate estimates of forest structural attributes using regressions have been successfully performed such as height [21,22], aboveground biomass [23,24], and crown diameter [25,26]. Lidar based biomass has been estimated for a variety of forest types including, but not limited to, temperate mixed deciduous coniferous [25,23,27], temperate deciduous [24] and tropical rain forests [28]. The third objective is to summarize forest structure of the predicted forest structural attributes for each mapped forest class. This step allows us to characterize forest height and biomass for different forest types on St. John and St. Thomas. The datasets generated in the project will support other studies in the Virgin Islands, including avian monitoring surveys and the Forest Stewardship Program [29].

2 METHODS

2.1 Study area

The US and British Virgin islands (18°20'N, 64°40'W) are a part of the Caribbean's Lesser Antilles and are composed of six major and 40+ minor islands and cays. The major islands in the US territory include St. Thomas, St. John and St Croix, while the main islands in the British territory include Tortola, Virgin Gorda and Anegada (Figure 1). The islands have a combined area of about 50,000 ha, with subdued to rugged topography and elevations ranging from just below sea level in some wetlands to over 500 m on the island of Tortola. The climate is mostly subtropical, with a hot and humid rainy season that extends from May to November and a dry season that is tempered by trade winds. The geology of the islands consists of alluvial, sedimentary, volcanic and limestone strata. Ecological zones on the islands include Subtropical Moist and Dry forest *sensu* Holdridge [1,30].

Lidar Study Area

St. John and St. Thomas were selected as the lidar study area based on the availability of lidar data coverage. The island of St. John (18°22'N, 64°40'W) and the island of St. Thomas (18°21'N, 64°55') are about 5,000 and 7,200 hectares in area, respectively, and consist of mountainous topography with elevations ranging from sea level to 387 m on St. John and 471 m on St. Thomas. The woody vegetation on both islands is similar to other islands in the Virgin Islands and includes both late and early stage successional forests.

In 1956, the US Park Service established the Virgin Islands National Park (VINP). Protecting about 65% of St. John, it includes the island's interior high elevation semi-evergreen and deciduous forests. The long standing reserve status has helped protect most of the island's forests from development, creating one of the largest contiguous expanses of forest in the Lesser Antilles. The VINP provides unique research opportunities to study the island's diverse ecology and establishes a template for monitoring mature successional forest structure. In contrast, the forests of St. Thomas which make up about 69% of the island has not received protection status and developmental pressures and impacts can be observed island-wide.

2.2 Landsat Imagery and Reference Data

A land-cover and forest type map for the US and British Virgin Islands was created by supervised classification of Landsat ETM+ imagery using decision tree analysis software. An image mosaic for about the year 2000 was created from Landsat scenes of various dates. The

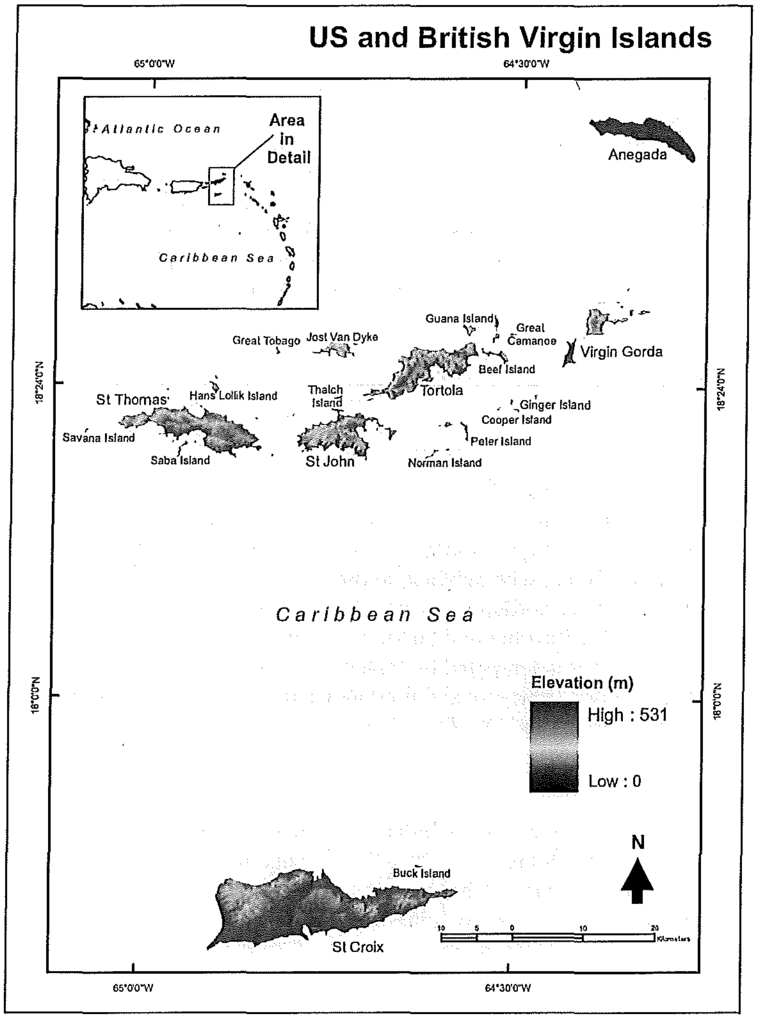


Fig. 1. Map of the study area.

reference scenes for the mosaic were World Reference System 2 Path/Row 004/047-048, both dated 27 Mar 00. The scenes used to fill cloud-masked or edge areas in Path/Row 004/047 were dated 02 Nov 01 (Path/Row 003/047), 17 Sep 99, 02 Aug 00, and 25 Jan 01. The scene used to fill cloud-masked areas in Path/Row 004/048, was dated 25 Jan 01. Cloud obstruction in the reference image was 20.9 % before and 5.3% after the cloud removal and mosaic process. The 30-m multispectral bands for each scene were first cloud-masked and then matched to the reference scene with regression tree normalization [31]. This technique models the relationship between co-located pixels from different image dates and estimates new image digital numbers (DNs) to fill in the cloud and cloud-shadow masked areas of the reference scene. In addition, the technique reduces atmospheric and phenological differences that occur with multi-date image mosaics [5]. Likewise, the 15-m panchromatic band for each scene was also matched to the reference panchromatic band with regression tree normalization models based only on the panchromatic bands. The matched panchromatic image parts were then mosaicked, and the panchromatic mosaic was then used to pan-sharpen the 30-m mosaic of the multispectral bands. Principal components transformation was chosen to merge the native 30 m Landsat multispectral image bands (bands1-5, 7) for each scene with the 15 m panchromatic band (band 8). It was chosen based on 1) results from preliminary tests of other resolution merging methodologies (Brovey and Multiplicative) available in ERDAS Imagine, and 2) other studies [32-34] that have concluded that the principle components transformation method provides increased spatial resolution without degrading spectral discrimination.

Ancillary data were used to create an island-wide predictor variable dataset to assist in the classification of image pixels. Adding geographic data ancillary to satellite imagery improves classification of land cover and forest types by reducing spectral confusion among vegetation classes [35,36], including in Caribbean island landscapes [6]. Topographic variables derived from United States Geological Survey (USGS) 30 m digital elevation models (DEM) for the US territory and 90 m Shuttle Radar Topography Mission (SRTM) elevation datasets resampled to 30 m for the British territory included elevation, slope and aspect [37,38]. Climatic variables included mean annual precipitation and temperature [39]. Variables derived from USGS Digital Line Graphics (DLG) for the US islands and scanned topographic maps for the British islands at a scale of 1:24,000 that were registered to the image mosaic include distance to primary and secondary roads, distance to streams and ravines, and distance to coastlines [40]. The ancillary predictor data was spatially co-registered with the cloud free image mosaic and stacked with the Landsat ETM+ reflectance bands 1-5, 7, and two band indices, resulting in an 18 band image mosaic for the classification. The band indices included the Landsat ETM+ image bands to produce the normalized difference vegetation index (NDVI) and 4/5 band ratio, which are useful indictors of vegetation vigor and forest structure [41-43].

Field surveys in 2005 and consultation with experts enabled us to discern land-cover and forest type in reference imagery and the classification image mosaic. The reference imagery included 1 m IKONOS panchromatic sharpened imagery for the US and British Islands and additional 1m color digital ortho quarter quads (DOQQ) for the US islands. Land cover and forest type were then identified in the satellite imagery. Forest type was identifiable in both the reference imagery and the Landsat imagery by color, tone and texture as well as spatial indicators including aspect and elevation. Difficulties distinguishing forest type were encountered in areas that were transitional between semi-deciduous and seasonal evergreen forest. Field survey data proved useful in identifying these transitional areas in the reference imagery.

Training data for the image classification model was derived using the reference imagery and field data collected in the 2005 reconnaissance survey. About 25 to 250 multiple pixel polygons were distributed for each class throughout the extent of the study area. Training data samples collected over a large inter-island extent ensured thorough representation of each class and provided a full range of variability for the class. For example, there are often spectral variations in similar forest types where the image scenes were radiometrically matched in the cloud elimination procedure [44]. Target classes included sunlit and shadowed woody vegetation types, sunlit and shadowed green and senescent pasture, mangrove, wetland, and non-forested classes (Table 1).

We used the woody vegetation classification system designated at the formation level (Table 1) that [45] adapted for Landsat imagery classification from [46]. Areas with less than

Table 1. Classification schema definitions including forest and non-forest classes.

Forest, forest/shrub, woodland and shrubland (Dry and Moist)	*Forest is defined as lands with > 25% cover of tree that co-dominate with shrubs*
Drought Deciduous Woodland	25-60% woody canopy cover with understory of grasses and forbs affected by grazing
Drought Deciduous Young Forest and Forest Shrub	Young drought deciduous secondary forest with Leucaena leucocephala and Acacia muricata common
Drought Deciduous Xeric Coastal Shrubland with Succulents	Very dry drought deciduous shrubland dominated by succulents and exposed soil and rock
Deciduous, Evergreen Mixed Forest and Shrubland with Succulents	Deciduous, drought deciduous and evergreen forest and shrub species (succulents common)
Evergreen Coastal Shrubland	Shrubland with > 75% evergreen species including hemi-sclerophyllous and sclerophyllous species
Semi-Deciduous Forest and Forest and Forest Shrub (Includes Semi-Evergreen Forest)	Stands with 25-75% deciduous woody canopy species
Semi-Deciduous Gallery Forest	Stands with 25-75% deciduous woody canopy species located in drainages
Seasonal Evergreen Forest and Forest Shrub	Stands with ≥75% evergreen woody canopy species (may drop leaves during drought)
Seasonal Evergreen Young Forest and Forest Shrub	Young seasonal evergreen secondary forest
Seasonal Evergreen Gallery Forest	Stands with ≥75% evergreen woody canopy species located in drainages
Seasonal Evergreen Forest with Coconut Palm	Stands with ≥75% evergreen woody canopy species dominated by coconut palm
Forested Wetland	
Mangrove	Mangrove forest
Seasonally Flooded Woodland	Disturbed forested wetland with 25-60% woody canopy cover and seasonal flooding or soil saturation
Agricultural land, pasture, hay, abandoned agriculture, grass	
Herbaceous Agriculture (Cultivated Lands)	Intensive agriculture and cultivated lands where activity is recent
Pasture, Hay, Abandoned Agriculture or other Grassy Areas	Areas with < 25% woody vegetation cover / recreation fields
Golf Course	Golf course
Coastal Grassland	Coastal grassland with < 25% woody vegetation
Non-forested and wetland	
Emergent Wetland	Emergent wetland permanent
Dry Salt Flats	Dry salt flats including mud flats
Quarries	Active or inactive quarries
Coastal Sand and Rock	Coastal sand (beaches) and coastal rock outcrops
Interior Rock (Virgin Gorda boulder)	Virgin Gorda rock outcrops (boulders)
Urban or built-up land	
High-Medium Density Urban	Land with > 80% urban features such as buildings, roads and impervious surfaces
Low-Medium Density Urban	Land with as low as 10-15% urban features and other land-cover types such as pasture or forest

25% woody vegetation cover are classified as pasture and grasslands; these include natural grasslands, abandoned agriculture and grazed or ungrazed pasture. Subtropical drought deciduous forest is defined by the Federal Geographic Data Committee (FGDC) as having at least 75% deciduous woody species [47]. Semi-deciduous forest [5] includes stands with 25-75% deciduous woody canopy species and includes semi-evergreen forest. Drought deciduous woodland has forest and shrub with a canopy cover of 25-60 % and an understory of grasses and forbs dominated by grazing or fire. Young leguminous secondary forest and shrub formations consisting primarily of *Leucaena leucocephala* and *Acacia muricata* were identified at lower elevations where recent or ongoing disturbance has occurred. Seasonal evergreen forest consists of at least 75% evergreen woody canopy species that may drop leaves during drought. Deciduous, evergreen and mixed forest with succulents includes a matrix of deciduous, drought deciduous and evergreen forest and forest shrub species containing succulents including *Stenocereus peruvianus, Leuchtenbergia principis and Opuntia tricantha.* Drought deciduous xeric coastal shrubland with succulents consists of very dry drought deciduous shrubland dominated by succulents and exposed or rocky soil. Evergreen coastal shrubland consists of a least 75% of evergreen species such as hemi-sclerophyllous *Coccoloba uvifera* and may include other sclerophyllous coastal shrub species. Low density urban land includes land with as low as 10-15% urban features and may include a mix of other land-cover types such as pasture, or forest. High-to-medium density urban land has greater than 80% urban features including buildings, roads and impervious surfaces.

2.3 Classification and Image Interpretation

See5 software (www.rulequest.com), a data mining program using decision tree algorithms, was used to predict land-cover and forest type pixel values [48]. In the last several years, decision tree classification techniques have been applied to a wide range of classification problems and have proven to be valuable to the classification of remote sensing imagery due to their flexibility, simplicity and computational efficiency [16,17]. First, a 10 trial adaptive boosting option was employed to improve the overall accuracy and reduce error of the decision tree algorithm by combining many individual classifiers (decision trees) into a single combined classifier [39]. Second, the default global pruning option was used to reduce the likelihood of over fitting the tree to the training data. The pruning process removes parts of the decision tree with relatively high error rates [49].

Manual editing of confused classes was required to correct for residual confusion between urban, barren and pasture areas. Several areas of drought deciduous young forest and drought deciduous woodland that were spectrally confused with pasture and grass were also manually edited. In addition, herbaceous agriculture on St. Croix was manually delineated, which accounted for 279 ha, or 0.01% of the total area mapped. Coastal grassland was manually recoded from pasture, including on small cays. Manual recoding was also necessary to delineate some drought deciduous young forest mostly on the island of St. Croix, and some boundaries between semi-deciduous and seasonal evergreen forest located on St. Thomas, St. John and Tortola. Coastal sand and rock was recoded throughout the classification. Finally, pixels were manually recoded in several high elevation areas of St. Thomas representing low density urban and a few areas of semi-deciduous and seasonal evergreen gallery forest. Areas in the image mosaic that were cloudy in all available Landsat images were manually interpreted from 1 m IKONOS panchromatic sharpened imagery and 1m color DOQQs (about 0.34% of the total mapping area).

2.4 Classification Accuracy Assessment

A stratified random sample was used to create 50 validation points for each land-cover class.

Each accuracy assessment point was verified with high resolution reference imagery and assigned a land-cover class. The reference imagery included IKONOS 1 m panchromatic sharpened imagery and 1m color DOQQs. An error matrix was created for each mapped class to estimate the overall percentage of correctly classified pixels, statistics for producer and user's accuracy and the Kappa coefficient, which is an indicator of the accuracy of chance agreement between classes [50,51]. Producer's accuracy is the proportion of correctly classified accuracy assessment estimates and user's accuracy estimates the proportional assignment of pixels to a correct class [5].

2.5 Lidar Data Processing

Discrete lidar data were collected during January and February 2004 by 3001 Inc. under contract to the US Army Corps of Engineers, using a Leica Geosystems ALS 40 sensor [52]. Geodetic control was established by a static GPS network covering the lidar survey area of Puerto Rico and the US Virgin Islands. In addition to data collection, Real-Time Kinematic GPS surveys were conducted to establish a network of ground truth data for statistical comparisons with the lidar data. The results of the comparisons indicate a Vertical Root Mean Square Error (RMSEz) of 9.26 cm on level smooth surfaces [52]. The spatial extent of the data in this study includes St. John and St. Thomas and surrounding small islands and cays. The lidar data were collected in conjunction with digital photos and used to generate and improve digital elevation models (DEM) for orthorectification. The raw point cloud data were provided by the contractor in .xyz format with a 2.76 m shot spacing and consists of multiple return measurements including first, last and intermediate return values.

The data were filtered into ground (minimum elevation) and non-ground returns to create a bare earth DEM and forest height estimates. TIFFS (Toolbox for Lidar Data Filtering and Forest Studies) was used to process the lidar data for extracting a bare earth DEM [53]. The filtering method used by TIFFS to create the DEM used a progressive morphological filter for removing non-ground measurements from the lidar elevation data [54]. Morphological filtering composes operations based on set theory to extract non-ground features from an image. The two fundamental operations include dilation and erosion which are used to enlarge (dilate) or reduce (erode) the size of features in continuous surfaces. By gradually increasing the window size of the filter and using elevation thresholds, the measurements of non-ground features such as vegetation and buildings are eliminated while topographic data are preserved [54]. The morphological filter algorithm used in [55] incorporates the assumption that non-ground objects such as buildings exhibit abrupt elevation changes while topographic elevation is gradual and continuous. This method is adaptive to local terrain and is applicable to rugged topography [53]. Once non-ground features were removed, terrain points were extracted from the approximated surface and a 5 m DEM was interpolated. Finally, the DEM tiles were mosaicked to form a continuous surface of the study area.

Programs written in IDL (Interactive Data Language, ITTVIS, 2008) were used to create a canopy height dataset from the non-ground elevation data [56]. The corrected DEM provided a minimum elevation surface which was subtracted from non-ground elevation lidar data to estimate canopy height. The resulting output was a continuous multiband image mosaic of canopy height variables with a 30 m pixel resolution. The image bands were of canopy height statistics including: (1) height percentiles (P-tile) below which certain percentages of data fall; (2) shot return profiles (SRP) that quantify the number of shots returned from 5 m height bins; (3) quadratic mean height (QMH) the root mean square of canopy lidar point height [57]; (4) maximum height; and (5) mean height (Table 2). Other areas where clouds obstructed the land and lidar measurements were treated as "no data". The cloud obstructed area was about 180 hectares or 1.4% of the study area and was confined mostly to the island of St. John. In addition, a water mask created from USGS 1:24,000 scale DLG data representing coastlines was used to mask ocean elevation measurements [40].

Table 2. USDA Forest Service, Forest Inventory and Analysis data, lidar and environmental variables.

FIA Plot Variables	**Units/Type**	**Definition**
Average Height of all Trees (AHT)	m	Average height of all trees
Average Height of Dominant/Co-dominant Trees (HDCD)	m	Average height of dominant and co-dominant trees
Above Ground Biomass per Hectare (AGBH)	Mg/ha	Above ground live biomass per hectare
Crown Volume (CV)	m^3	Sum of the volume of all crowns for trees with a d.b.h. ≥ 12.5 cm. Estimated as an ellipsoid using crown ratio, tree height and crown radius in two perpendicular directions (V= 4pi/3)abc
Lidar Variables		
Minimum Elevation	m	Minimum lidar surface elevation
Maximum Height	m	Maximum lidar canopy height
Mean Height	m	Mean lidar canopy height
Quadratic Mean Height (QMH)	m	Root mean square height of the lidar points
Height Percentiles (P-tile)	m	Height at which a certain percent of data fall below
Shot Return Profile (SRP)	m	Number of shots returned from 5 meter height bins
Environmental Variables		
Landsat Bands 1-5, 7	Integer	Landsat image reflectance bands
Landsat NDVI, 4/5 Ratio	Float	Normalized Difference Vegetation Index, Band 4/Band 5
Aspect	Degrees	Aspect expressed in degrees
Sine Aspect	Radians	Sine of aspect in radians
Cosine Aspect	Radians	Cosine of aspect in radians
Curvature	Integer	Slope geometry indicating convex or concave geometry
Slope	Degrees	Slope expressed in degrees
Slope Position	Integer	Ridge or valley of any point in landscape
Degrees from North	Degrees	Degrees from 0 (north)
Landsat Classification	Nominal	Land-cover and forest type thematic values
Precipitation	mm/year	Total annual precipitation
Temperature	mm/year	Mean annual temperature

2.6 Forest Parameter Modeling

Regression models of field estimated canopy height and biomass were developed from lidar estimates of canopy height and environmental variables. The plot data was collected by the USDA Forest Service Forest Inventory Analysis (FIA) Caribbean program on St. John and St. Thomas in 2004 [58] providing field based forest structural information (Table 2). Each plot consists of four 7.3 m radius circular subplots in which all woody vegetation with a diameter at breast height (DBH, measured at 1.37 m) of ≥ 12.5 cm is surveyed. A single microplot with a 2.1 m radius nested within each subplot is used to survey woody vegetation saplings with a DBH between 2.5 and 12.5 cm [59]. Summary statistics were generated at the plot and subplot level. For the plot level data, circular and square plot extraction schemes were used to extract the lidar mosaic data using a 90 m window. In addition to the lidar data, this study examined if other explanatory variables such as ancillary environmental data improved the regressions and fit of the models of structural data (Table 2). Ancillary data included Landsat reflectance bands (bands 1-5, 7) and band indices (NDVI and the ratio of bands 4 and 5), total annual precipitation and mean annual temperature (Helmer, Daly and Plume, unpublished data), land-cover and forest type, and elevation and elevation derivatives such as slope, aspect, and sine and cosine of aspect expressed in radians. Two other topographic indices were included: slope position, which calculates the extent that each point is similar to a ridge or valley position as values 0 through 100 [60], and standard curvature, which is a measure of slope geometry indicating convex or concave topography [61]. A 24 band image stack containing the lidar canopy height statistics and the environmental variables was assembled, and data were extracted at every FIA plot and subplot location. The sample size for the plot and subplot level data was 18 and 72 observations respectively.

We developed stepwise regression models in JMP software (www.sas.com) and used the resulting regression equations to create images of predicted values with a 30 m pixel resolution for average height of dominant and co-dominant trees (HDCD), and above ground biomass per hectare (AGBH) on the islands of St. John and St. Thomas [62] (Table 3). Forest structural statistics were then calculated using a zonal operation for the predicted maps of HDCD and AGBH and related to the areas of the forest types mapped in the land-cover classification for St. John and St. Thomas.

3 RESULTS

3.1 Land-cover and Forest Type Classification

The land-cover and forest type classification consisted of 29 classes (Figure 2 and Appendix A and B). After manual editing and interpretation of residual cloudy areas the overall accuracy was 72%. The Kappa coefficient of agreement was 0.76 ± 0.01, which indicates a significant agreement between the reference and map classifiers. The main sources of error were confusion between low density and high-medium density urban lands, and between low density urban lands and pasture. Most of the forest types were classified with greater than 70% accuracy (Appendix A). However, some confusion occurred between semi-deciduous forest and seasonal evergreen forest. Also, deciduous, evergreen and mixed forest and shrubland with succulents showed some confusion with semi-deciduous forest, drought deciduous young forest shrub and woodland classes.

Table 3. Stepwise regression equations for forest structural response variables using Forest Inventory Analysis fully forested plot level data for the islands of St. John and St. Thomas. The predicted models are significant at $p< 0.05$ and 18 observations. Superscript symbols indicate significance levels of overall model: $^{\circ}$ ($p\leq 0.0001$), $^{+}$ ($p\leq 0.001$), $^{\Delta}$ ($p\leq 0.05$)

Response variable	Explanatory data (lidar / environmental variables)[1]	Predicted model	RMSE	Adj. R^2
Average height of dominant/co-dominant trees (HDCD)	SRP 2, SRP 6, PRECIP$^{\circ}$	HDCD = -14.03+ 10.67(SRP2) + 24.10(SRP6) + 0.00015(PRECIP)	0.78	0.73
Above ground biomass per hectare (AGBH) mapped	SRP 5$^{\Delta}$	AGBH = 58.29 + 220.17(SRP5)	22.78	0.36
Above ground biomass per hectare (AGBH) mapped	Observed HDCD^{+}	AGBH = -22.92 + 14.27(Observed HDCD)	15.29	0.72[2]
Above ground biomass per hectare (AGBH) mapped	Predicted HDCD$^{\Delta}$	AGBH = -9.89 + 12.37(Predicted Formula HDCD)	22.69	0.37[2]
Average height of all trees (AHT)	MEANH, COSAP, LSB 1, 5, 8$^{\Delta}$	AHT = 3.14 + 0.35(MEANH) + 0.69(COSAP) - 0.13(LSB1) - 0.084(LSB5) + 0.48(LSB8)	0.75	0.59
Crown volume (CV)	SRP 2, SRP 6, COASP^{+}	CV = 87.44 – 646.612(SRP4) + 1959.04(SRP6) + 76.69(COASP)	51.48	0.77
Height Penetration Index (HPI)	ASPECT, SLOPE, SLPPOS, PRECIP$^{\Delta}$	HPI = -0.87 - 0.0006(ASPECT) – 0.005(SLOPE) + 0.002(SLPPOS) + 1.28e-5(PRECIP)	0.09	0.56

[1] Lidar variable definitions: SRP (Lidar Shot Return Profile), PRECIP (Average Annual Precipitation mm/yr), MEANH (Lidar Mean Canopy Height), COSAP (Cosine of Aspect in radians), LSB (Landsat TM Band (band 8 = 4/5 ratio)), SLOPE (Slope in degrees), ASPECT (Aspect in degrees), SLPPOS (Slope position).

[2] Linear equations are stated in R2

Confusion among these classes can be explained by similarities in deciduous and drought deciduous forest shrub and woodland species. Finally, some confusion occurred between pasture, drought deciduous woodland and drought deciduous young forest shrub. Pasture often exhibits confusion with drought deciduous forest types in Landsat classifications due its composition of up to 25% drought deciduous woody vegetation species [5]. The mapped combined closed woody vegetation (closed forest and associated classes) for the seven main islands and their associated islets and cays, was 34,175 ha, which encompassed about 67.7% of the total mapped island area (Appendix A). Pasture, hay, abandoned agriculture or other grassy areas was the second most abundant class representing 12.2% of the total mapped area. The total urban and developed land area was about 6,367 ha in 2000 (Appendix B).

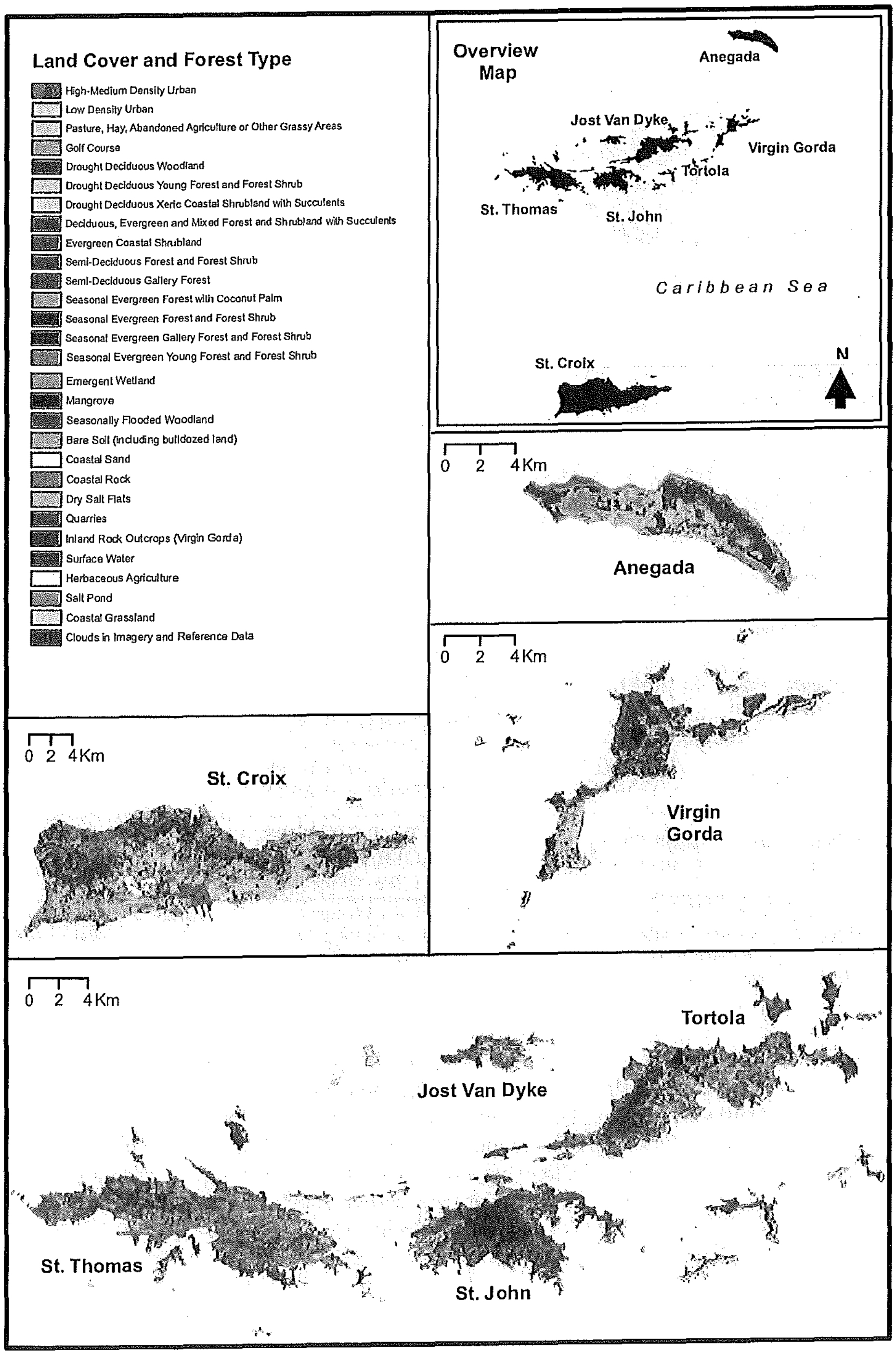


Fig. 2. Land cover and forest type classification for the United States and British Virgin Islands

3.2 Lidar Data Processing

The TIFFS algorithm efficiently filtered the large volume of point cloud data, although the processing required manual parameter tuning and multiple iterations to produce an adequate DEM. The mean shot spacing was one shot per 2.76 m. Mean canopy height ranged between 2.0 and 16.9 m with a mean and standard deviation of 5.4 and 2.2 m. The mean canopy height image with outliers removed shows a realistic representation of mature moist forest stands and short drought deciduous and xeric forest types. The minimum and maximum value of the elevation image before correction was -82.4 and 970.7 m with a mean and standard deviation of 14.0 and 48.3 m respectively. After correction using the TIFFS software, the minimum and maximum bare earth DEM values were -4.094 and 470.5 m with mean and standard deviation of 3.3 and 68.6 m. Negative values resulted from ocean shots that were not completely removed in the masking process due to minor edge matching differences in the water mask and the lidar data.

3.3 Estimating and Modeling Forest Structural Parameters

Models at both the plot and subplot levels that used only lidar indices were statistically significant but did not explain as much variance as other studies using lidar (adjusted R^2 for plot level HDCD = 0.49 and RMSE 1.07 m; adjusted R^2 value for subplot level HDCD = 0.18 and RMSE 1.79 m). Further data analysis indicated the existence of a regular pattern between the regression residuals, canopy closure and environmental conditions. To quantify these effects, we calculated a height penetration index as an indication of the distance that the lidar penetrated through the forest canopy. The height penetration index is defined as average height of dominant and co-dominant trees divided by lidar maximum height. Values of this index near 1.0 represent canopies where most returns are from dominant and co-dominant trees; values greater than 1.0 indicate higher level of penetration into the canopy. A stepwise regression of the height penetration index and related environmental variables show a strong dependence (adjusted R^2 = 0.56, Table 3). The environmental variables that were significant in the regression include aspect, slope, slope position and precipitation and are a major component of environmental gradients found in Caribbean landscapes that influence forest types and structure. Given the direct relationship between environmental variables and this characteristic of forest canopy structure, environmental variables were added as dependent variables.

Models of forest structural parameters that included environmental variables were significant at both the plot and subplot level, but plot level relationships explained more variance. For example, the adjusted R^2 value was 0.40 for the model of subplot HDCD but 0.73 for the plot level model. At the plot level, plot extraction using circular and square sample areas both provided statistically significant models, but the circular plot scheme explained more variance (adjusted R^2 for HDCD circular plot = 0.73; adjusted R^2 for HDCD square plot = 0.59).

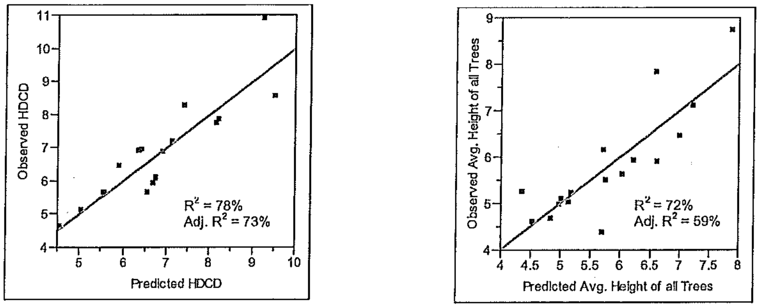
The relationships between the lidar and environmental variables, and the inventory plot level measurements of HDCD are strong, but most of the environmental variables tested were insignificant. Regressions of HDCD with lidar shot return profile (SRP) variables and precipitation explain high levels of variance, with an adjusted R^2 of 0.73 (Table 3, Figure 3). The RMSE of 0.78 m for HDCD is 11.35% of the response mean of 6.87 m which is a relatively low error. The regression equation for HDCD is dependent on the explanatory variables shot return profile 2 (SRP2), shot return profile 6 (SRP6) and the environmental variable total annual precipitation resulting in the following multiple regression model with all explanatory variables significant at $p<0.05$ (Table 3):

$$HDCD = 14.03 + 10.66SRP2 + 24.10SRP6 + 0.00015PRECIP \quad (P < 0.0001) \qquad (1)$$

The predicted model for inventory HDCD explained a greater amount of variance and produced a more reasonable height map than did the equation for predicted Average Height of all Trees variable (adjusted $R^2 = 0.59$, Table 3). This suggests that the coarse resolution lidar is more sensitive to the height of the dominant and co-dominant trees than the average height of all trees and can be attributed to the inability of the lidar returns to account for the variability of the forest understory.

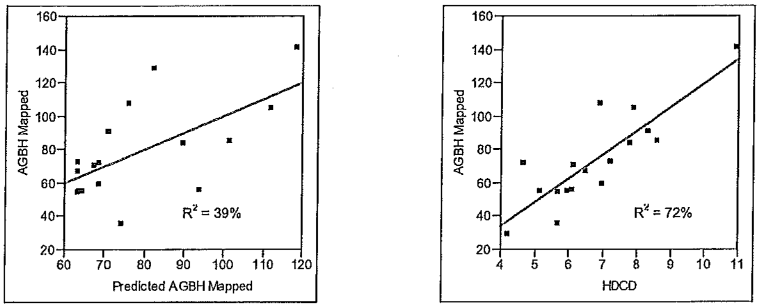
Average Height of Dominant and Co-dominant Species (m)

Average Height of all Trees (m2)



Above Ground Biomass/Hectare (Mg/ha)

Above Ground Biomass/Hectare (Mg/ha) Bivariate AGBH Mapped By HDCD



Crown Volume (m3)

Above Ground Biomass/Hectare (Mg/ha) Bivariate AGBH Mapped By Predicted HDCD

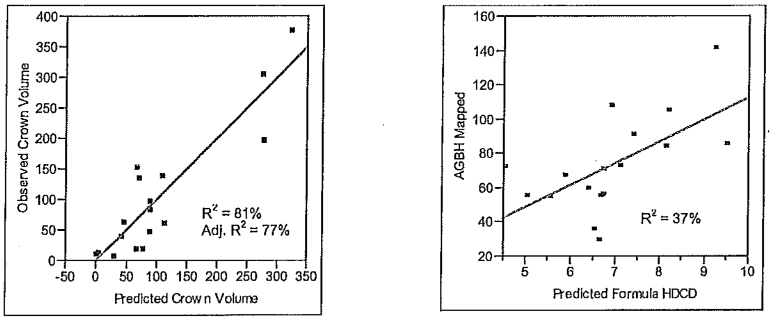


Fig. 3. Graphs of predicted versus observed forest structural variables

The relationship between the lidar data, environmental variables, and the inventory plot level measurements of AGBH explain only 36% of the variance. No environmental variables were significant and SRP 5 was the only significant explanatory variable in overall model with a p-value of 0.01 (Table 3). The model did not adequately map low biomass values in dry forest and forest shrub formations and did not consistently map biomass values in adjacent tall and short forested areas. Instead, an alternative approach that uses the strong relationship between AGBH and HDCD in the inventory plot dataset was applied. A bivariate fit between inventory HDCD and AGBH results in the following linear regression model explaining 72% of the variation with RMSE (15.29 m) (Table 3, Figure 4).

$$\mathrm{AGBH} = -22.92 + 14.27\mathrm{HDCD} \qquad (P < 0.0001) \tag{2}$$

The map of the AGBH model shows the same trends as the predicted map of HDCD due to their direct linear dependence. Biomass estimates generally increase with an increase in elevation and canopy height (Figure 4). A few areas of predicted biomass located primarily in the island's high elevation ridge topography were estimated beyond the maximum range of the observations that form the regression model and exceeded values reasonable for subtropical moist forest in the region. A threshold was determined based on the largest biomass estimate (141.3 Mg/ha) from FIA plot data located in St. John. Predicted estimates exceeding the threshold were reclassified in the map to this maximum value. Larger biomass estimates are not reported on St. John, though dense mature moist forest stands in the drainages could show values exceeding the threshold. Modeled biomass values that exceed the range of reasonable observations occur on high elevation ridges; a location where biomass is unlikely to be near the FIA maximum. [63] summarized biomass estimates of Caribbean dry and moist forest from recent studies showing values for the Cinnamon Bay watershed measured after hurricane Hugo in 1989 to be about 131.5 tons/ha. Finally, [64] presents pre-hurricane Gilbert average biomass estimates for Rancho San Filipe, Mexico of 132 Mg/ha in forests similar to St. John, but consisting of drier forest types. In addition, a few low elevation areas consisting of mostly drought deciduous xeric coastal shrubland with succulents were modeled in the AGBH map with negative values due to the y intercept of the model at about 1 m. To correct this error, a minimum biomass estimate threshold was applied to the negatives values based on a minimum HDCD height of 1.2 m.

The relationship between the lidar data, environmental variables, and the inventory plot level measurements of Crown Volume explain 81% of the variance with RMSE (51.48 m). Although, crown volume was accurately estimated in the regression models, the predicted maps provided a poor representation of this variable throughout the study area showing large non-contiguous areas of negative and erroneous values at both high and low elevations and therefore not included as a final predicted map.

3.4 Forest Structural Summaries

Forest structural summaries derived from the predicted maps for HDCD and AGBH show height and biomass statistics for the islands of St. John and St. Thomas and include mapped drought deciduous, xeric and coastal classes located on the surrounding small islands and cays (Tables 4A and B). The mean height and biomass estimates are similar to FIA field estimates of moist forest types. Height and biomass estimates for seasonal evergreen, and semi-deciduous forest show a slight increase in the maximum and mean forest height and total biomass in St. John compared to St. Thomas in protected areas. This result may show the effect of the protected status of seasonal evergreen and semi-deciduous forest within the

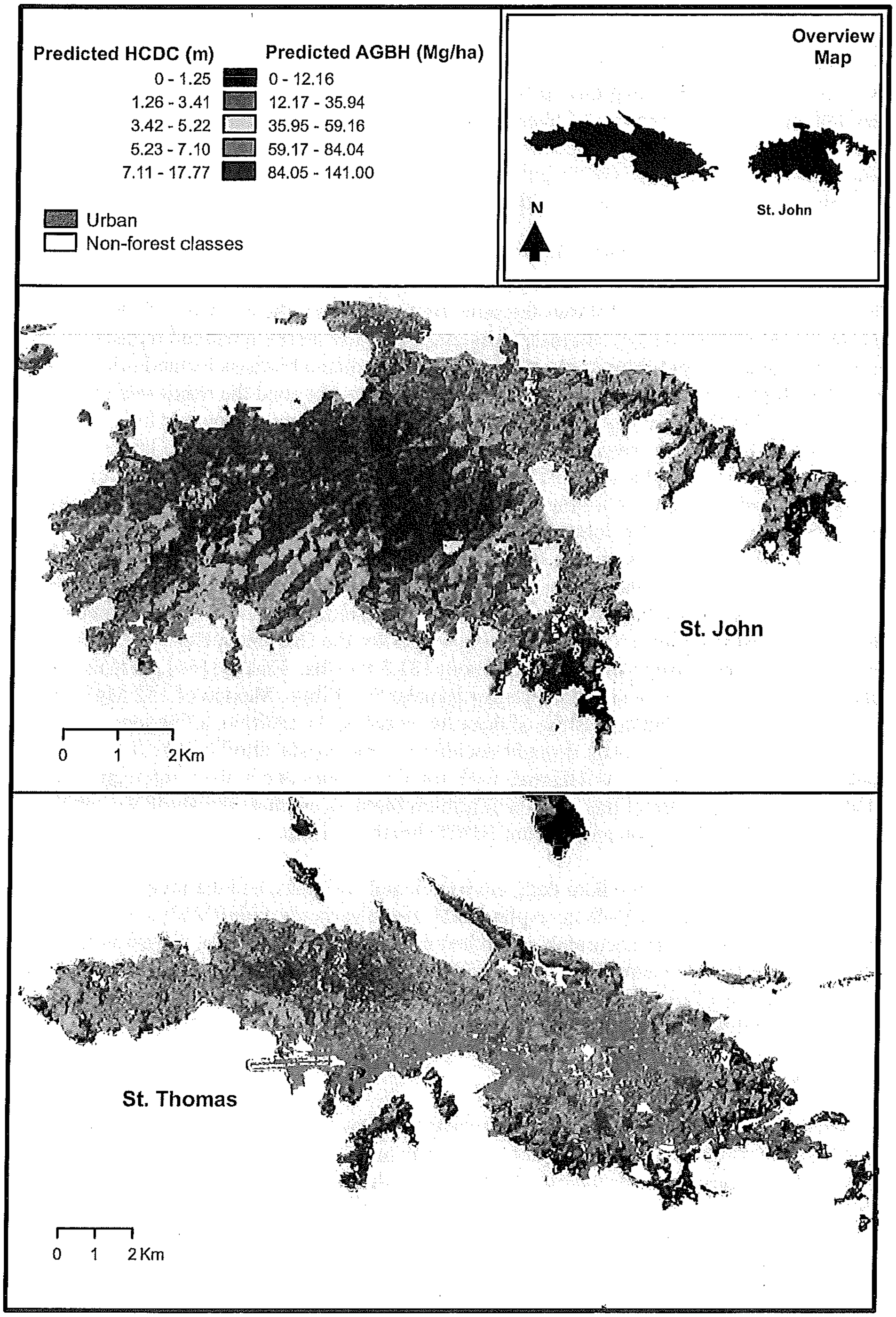


Fig. 4. Map of predicted average height of dominant and co-dominant trees (HDCD) and above ground biomass per hectare (AGBH) for the islands of St. John and St. Thomas.

VINP where these larger height values are identified. Drought deciduous xeric coastal shrubland and evergreen coastal shrubland has the smallest mean HDCD and AGBH estimates and show reasonable values for the short shrubland classes. Mean HDCD estimates for the largest dry forest formation, deciduous evergreen mixed forest and shrubland with succulents was 4.4 m for St. John and 3.0 m for St. Thomas with mean AGBH estimates of 39 Mg/ha and 21 Mg/ha respectively.

Table 4A. Forest structural summaries for average height of dominant and co-dominant trees for the mapped forest types on St. John and St. Thomas including surrounding small islets and cays. Slight discrepancies in forest type area between the predicted lidar maps and the land-cover classification are due to "no data" masks in the lidar data.

Average height of dominant and co-dominant trees (HDCD) (m)	**St. John**				**St. Thomas**			
Forest formation mapped	Min	Max	Mean	STD	Min	Max	Mean	STD
Drought Deciduous Woodland	-	-	-	-	1.3	6.9	3.4	1.8
Drought Deciduous Young Forest and Forest Shrub	1.9	11.0	4.3	1.5	0.1	12.2	3.1	1.7
Drought Deciduous Xeric Coastal Shrubland with Succulents	1.3	9.1	2.7	1.4	0.0	10.8	2.0	1.4
Deciduous, Evergreen Mixed Forest and Shrubland, with Succulents	1.3	13.9	4.4	1.6	0.0	12.2	3.0	1.6
Evergreen Coastal Shrubland	1.1	9.5	2.9	1.3	0.0	7.8	2.3	1.5
Semi-Deciduous Forest and Forest Shrub	1.5	15.6	6.2	1.4	0.6	13.6	4.8	1.4
Semi-Deciduous Gallery Forest	2.2	12.5	5.9	1.6	1.7	11.4	5.4	1.3
Seasonal Evergreen Forest and Forest Shrub	4.0	16.1	7.5	1.2	2.9	13.1	6.6	1.3
Seasonal Evergreen Young Forest and Forest Shrub	5.5	8.6	6.0	1.1	4.0	8.3	4.5	1.1
Seasonal Evergreen Gallery Forest	3.4	15.5	7.3	1.5	2.1	13.0	6.2	1.2
Seasonal Evergreen Forest with Coconut Palm	3.7	10.7	7.4	1.5	1.5	10.1	5.8	1.4
Mangrove	1.4	9.4	4.8	1.6	0.0	9.8	2.7	1.9
Seasonally Flooded Woodland	1.9	9.2	4.4	1.5	1.3	10.7	3.7	2.2

Table 4B. Forest structural summaries for above ground biomass per hectare for the mapped forest types on St. John and St. Thomas including surrounding small islets and cays. Slight discrepancies in forest type area between the predicted lidar maps and the land-cover classification are due to "no data" masks in the lidar data.

Above ground biomass per hectare (AGBH)	**St. John (Mg/ha)**				**St. Thomas (Mg/ha)**				**Both islands**
Forest formation mapped	Min	Max	Mean	STD	Min	Max	Mean	STD	Total (Gg)
Drought Deciduous Woodland	-	-	-	-	1	75	27	24	0
Drought Deciduous Young Forest and Forest Shrub	4	134	39	21	0	141	24	22	131
Drought Deciduous Xeric Coastal Shrubland with Succulents	0	108	17	18	0	132	11	16	34
Deciduous, Evergreen Mixed Forest and Shrubland, with Succulents	0	141	39	23	0	141	21	20	1,057
Evergreen Coastal Shrubland	0	112	19	18	0	88	14	18	22
Semi-Deciduous Forest and Forest Shrub	1	141	65	20	0	141	46	20	2,426
Semi-Deciduous Gallery Forest	8	141	61	22	1	140	54	19	65
Seasonal Evergreen Forest and Forest Shrub	34	141	84	17	18	141	71	19	1,088
Seasonal Evergreen Young Forest and Forest Shrub	55	100	77	15	34	95	62	15	4
Seasonal Evergreen Gallery Forest	25	141	81	20	7	141	66	18	262
Seasonal Evergreen Forest with Coconut Palm	30	130	81	21	1	121	59	20	14
Mangrove	0	111	45	23	0	118	19	25	43
Seasonally Flooded Woodland	4	108	40	21	1	129	31	31	5

4 DISCUSSION

4.1 Land-cover Classification Techniques

The use of decision tree classification techniques to map land cover and forest types in subtropical environments has been highly successful in past studies [17,4,5]. This study uses the techniques tested in previous work to create the first Landsat ETM+ land-cover and forest type classification for the US and British Virgin Islands. Unique to this study is that for the first time we created 15-m panchromatic-sharpened cloud-free mosaics and used them in a classification to simultaneously map land-cover and forest types over a large inter-island extent.

The classification approach provided several advantages over traditional techniques in this study area. First, the Principal Components transformation for creating 15 m panchromatic sharpened Landsat imagery was effective for increasing the spatial resolution of the Landsat multi-spectral bands. The resulting imagery enhanced the ability to discern sparsely vegetated surfaces, urban features in low density urban areas and linear features such as riparian corridors. However, difficulty in distinguishing areas of less than a few pixels, like very small forest patches, small clearings, or man-made structures in forest still proved difficult due to the moderate resolution of the panchromatic sharpened imagery.

The second advantage of this approach was the utility of the mostly cloud-free image mosaic for training data collection and classification. The technique devised by [6] provided a repeatable method for replacing the cloudy areas with images from different dates in which vegetation phenology is generally normalized to the base scene. This process makes training data collection in the cloud-filled areas easier by providing a single image mosaic with minor differences in image tone [5].

4.2 Estimating and Modeling Forest Structural Parameters

Stepwise regression was effective for estimating canopy height, as measured in FIA plot data, from lidar canopy height estimates and environmental variables. Testing different multiple regression models showed that the large point spacing of the coarse resolution lidar is most suitably modeled at the plot level, with a 90 m window circular plot extraction design. In addition, the large point spacing of the lidar data is most appropriate for height measurements of dominant and co-dominant trees, due to the inability to accurately measure forest understory. This limitation is the most likely reason why the models of above ground biomass per hectare were inaccurate. A significant portion of the biomass in Caribbean landscapes is located in the forest understory and contributes greatly to overall biomass estimations. The proportion of biomass contribution decreases with an increase in average tree height and is calculated to be about 94% based on a FIA plot with an HDCD of 4.1 m and 24% for a FIA plot with a HDCD of 10.9 m. This assumption is further supported by a stepwise regression using lidar and environmental variables to estimate field measurements of above ground biomass that don't include the biomass contribution measured on microplots (trees and shrubs with diameters < 12.5 cm). The regression to estimate biomass without the microplot contribution was significantly related to lidar SRP 1, SRP 6, QH and Landsat TM band 1, explaining 81% of the variance compared to only 36% of the variance for AGBH with scaled micro plot. This supports the conclusion that the coarse resolution of the lidar data is more sensitive to the larger dominant forest structure located in the upper canopy.

The regression equation for the "Height Penetration Index" and the importance of environmental variables for predicting forest structure suggests that canopy structure varies substantially with environmental conditions in this study area. Field observations and photo interpretation show how forest structure on these islands changes with aspect and elevation, which also influence solar input, wind, and climate. Because of these interactions, estimating/mapping forest structure in Caribbean environments may require stratification of field plots by forest type, which will increase the cost of field work for these studies by the number of strata. In this study, which used FIA data collected with systematic sampling, we did not have this variety of sites across the main environmental gradient. An alternate sampling scheme should allow the appropriateness of using environmental variables in this way.

The HDCD and AGBH models yield reasonable maps of those variables for St. John and St. Thomas across the range of elevations, showing a trend of increasing canopy height and biomass with an increase in elevation (Figure 4). Field observations and reference data confirm the mapped results, which show taller forest stands associated with higher elevations as well as slopes and drainages sheltered from prevailing winds and solar radiation. Canopy height and biomass estimates on windward south and southeast aspects are smaller than those on lee slopes. While most low lying areas with relatively short forest types are accurately predicted in the HDCD model, several short forest types estimated adjacent to coastal areas, including drought deciduous xeric shrubland with succulents and evergreen coastal shrubland, have scattered pixels that exceed reasonable heights. This result may be due to isolated large trees, land-cover classification errors, or lidar height errors from non-forest features. Also, a few of the large watershed drainages in the predicted maps show taller forest stands and larger biomass estimates than have been identified in FIA surveys and reference imagery, while some of the watershed drainages at lower elevations depict height estimates that may be too short (Figures 2 and 4). This discrepancy may be caused by high density forest structure and the inability of the lidar to penetrate the canopy to estimate accurate minimum elevation data or the lack of multiple returns for the lidar data in some areas. Flat urban features such as recreation fields, golf courses, and the St. Thomas airport runway as well as some pasture are predicted as zero height in the maps, although urban features such as buildings depict reasonable height estimates.

The forest structural summaries provide a quantitative overview of the average height and biomass of the forest types in the study area. Seasonal evergreen and semi-deciduous forests including gallery forests, which represent the dominant moist forests on St. John, and St. Thomas, had the largest mean height and biomass. Semi-deciduous forest on both islands accounted for the largest total combined biomass. These moist forest types contain the tallest forest stands and greatest biomass, providing an indicator of structure, species richness and habitat suitability, and highlighting their importance for protection status. Mean maximum height and biomass for seasonal evergreen forest and semi-deciduous forest are slightly larger on St. John compared to St. Thomas, especially for the seasonal evergreen forests that are well represented under protection status (Table 4A and B). In contrast, drought deciduous xeric coastal shrubland with succulents and evergreen coastal shrubland forest types depict the smallest mean height and biomass estimates. Low elevation deciduous evergreen mixed forest and shrubland with succulents represents the largest biomass estimate for the dry (drought deciduous) forest types. Incidentally, in the Caribbean, the unprotected low elevation dry forests represent the greatest danger of deforestation due to increasing developmental pressure and are considered critical habitat for many endemic vegetation species and important habitat for Neotropical migratory birds [65].

Prior to this study, applications for low density lidar data include topographic modeling, feature extraction and floodplain and coastal mapping [66,67]. For example, the Louisiana Statewide Lidar Project was initiated due to increased flood loss rates experienced by the FEMA National Flood Insurance Program and provides low cost lidar derived high resolution topographic data to update floodplain maps [67]. The project incorporates the Leica Geosystems ALS 40 lidar mapping system used in this study with 3 m point spacing and the subsequent acquisition of aerial photography to develop products pertaining to floodplain mapping at a regional and watershed scale. While the use of coarse resolution discrete lidar to map topographic features is known, this study shows new applications for this type of data providing a cost effective technique to map forest structure in a subtropical environment that can be applied to forestry applications in other settings.

5 CONCLUSION

Decision tree classification using cloud free image mosaics of panchromatic sharpened Landsat ETM+ images proved effective for mapping land cover and forest types in the Virgin Islands providing more detail than previous mapping efforts. The overall accuracy of the 29 forest and non-forest classes was 72%, with most of the forest types classified with greater than 70% accuracy. The mapped combined closed woody vegetation for the seven main islands and their associated islets and cays, was 34,175 ha, which encompassed about 67.7% of the total mapped island area.

The coarse resolution discrete lidar data accurately modeled forest structure including average height of dominant and co-dominant trees, average height of all trees and above ground biomass per hectare on the islands of St. John and St. Thomas, where forest types vary dramatically with topography and environmental factors. However, due to the large point spacing, the lidar data is more indicative of upper canopy dominant and co-dominant tree height as opposed to the average height of all trees. The data did not completely account for variability in the forest understory. This limitation prevents accurate biomass estimates using a stepwise regression approach due to lack of important understory contributions of woody vegetation. However, as this study concludes, biomass can be estimated by its direct relationship with canopy height.

This study shows that mapping forest height and biomass can be performed from coarse resolution discrete return lidar sensors in Caribbean landscapes. The resulting quantification of forest structure enables better characterization of the forest types from a passive optical image classification. In addition, this study shows that regression modeling of forest height and biomass can be performed using limited plot data that does not represent the complete range of height values found in the forest types. Another major advantage of this type of lidar data is the relatively low cost of data acquisition, because this type of data are often collected in conjunction with high resolution airborne digital photos. Additional studies are necessary to further test how field plot sampling design may improve the models. This may include stratification of field plots by forest type, accounting for a comprehensive range of heights for each environmental condition. However, this approach will increase the cost of field work based on the number of strata assigned.

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Appendix A. Forest and non-forest areas including the User's and Producer's accuracies for the 2000 U.S. Virgin Islands land-cover and forest type classification. Area totals rounded to integer values (Area totals include small islands and cays associated with major islands).

Forest and non-forest classification name	User's Accuracy[1] (%)	Producer's Accuracy[1] (%)	St. Croix (ha)	St. John (ha)	St. Thomas (ha)	Total Area (ha)
Forest, forest/shrub, woodland and shrubland						
Drought Deciduous Woodland	63	81	409	0	1	554
Drought Deciduous Young Forest and Forest Shrub	70	54	2974	190	211	3499
Drought Deciduous Xeric Coastal Shrubland with Succulents	73	62	93	85	160	473
Deciduous, Evergreen Mixed Forest and Shrubland, with Succulents	84	60	6153	1558	1794	9649
Evergreen Coastal Shrubland	82	79	117	44	101	423
Semi-Deciduous Forest and Forest Shrub	77	65	1770	1584	2587	6083
Semi-Deciduous Gallery Forest	74	90	528	41	64	797
Seasonal Evergreen Forest	84	72	0	783	453	1392
Seasonal Evergreen Young Forest and Forest Shrub	62	88	0	1	6	157
Seasonal Evergreen Gallery Forest	76	85	128	175	147	611
Seasonal Evergreen Forest with Coconut Palm	78	95	1	11	8	193
Forested Wetland						
Mangrove	83	66	185	48	105	487
Seasonally Flooded Woodland	59	81	0	8	4	152
Urban or built-up Land						
High-Medium Density Urban	78	78	2747	80	1040	4023
Low-Medium Density Urban	68	67	399	219	798	1551
Agricultural Land, Pasture hay abandoned agriculture or other grassy areas						
Herbaceous Agriculture – Cultivated Lands[1]	86	100	275	0	0	461
Pasture hay abandoned agriculture or other grassy areas (i.e. soccer fields)	74	55	5173	54	261	5617
Golf Course	89	95	86	0	28	298
Coastal Grassland	70	83	53	17	39	262
Non-forested and Wetland						
Emergent Wetlands	66	89	12	1	17	185
Dry Salt Flats (Includes mud flats)	76	81	135	9	2	303
Quarries	94	98	62	0	28	282
Coastal Sand	79	89	104	38	35	345
Coastal Rock	61	87	61	96	242	547
Interior Rock (Virgin Gorda boulder)	74	89	0	0	0	163
Bare Soil (including bulldozed land)	78	89	37	5	16	225
Salt Pond	90	75	232	42	20	459
Surface Water	80	97	61	1	3	242

[1] User's and producer's accuracies include both US and British Virgin Islands

Appendix B. Forest and non-forest areas for the 2000 British Virgin Islands land-cover and forest type classification. Area totals rounded to integer values (Area totals include small islands and cays associated with major islands).

Forest and non-forest classification name	Anegada (ha)	Jost Van Dyke (ha)	NPCG[1] (ha)	Tortola (ha)	Virgin Gorda (ha)	Total Area (ha)
Forest, forest/shrub, woodland and shrubland						
Drought Deciduous Woodland	643	0	0	1	8	652
Drought Deciduous Young Forest and Forest Shrub	440	157	69	454	109	1229
Drought Deciduous Xeric Coastal Shrubland with Succulents	28	103	162	68	209	570
Deciduous, Evergreen Mixed Forest and Shrubland, with Succulents	841	422	464	2044	808	4579
Evergreen Coastal Shrubland	544	12	28	90	82	756
Semi-Deciduous Forest and Forest Shrub	0	156	30	1824	637	2647
Semi-Deciduous Gallery Forest	0	3	0	29	22	54
Seasonal Evergreen Forest	0	0	0	633	38	671
Seasonal Evergreen Young Forest and Forest Shrub	0	0	0	149	0	149
Seasonal Evergreen Gallery Forest	0	0	0	87	0	87
Seasonal Evergreen Forest with Coconut Palm	0	0	1	4	3	8
Forested Wetland						
Mangrove	91	4	2	68	10	175
Seasonally Flooded Woodland	0	0	0	10	0	10
Urban or built-up Land						0
High-Medium Density Urban	6	5	3	303	47	364
Low-Medium Density Urban	107	28	12	426	147	720
Agricultural Land, Pasture hay abandoned agriculture or other grassy areas						
Herbaceous Agriculture – Cultivated Lands[1]	0	0	0	5	0	5
Pasture hay abandoned agriculture or other grassy areas (i.e. soccer fields)	78	31	63	376	135	683
Golf Course	1	0	0	0	0	1
Coastal Grassland	7	35	47	22	40	151
Non-forested and Wetland						
Emergent Wetlands	0	0	0	3	0	3
Dry Salt Flats (Includes mud flats)	581	1	3	11	2	598
Quarries	0	0	0	11	4	15
Coastal Sand	98	10	18	36	25	187
Coastal Rock	9	67	165	128	107	476
Interior Rock (Virgin Gorda boulder)	0	0	1	0	20	21
Bare Soil (including bulldozed land)	0	0	1	16	3	20
Salt Pond	514	1	7	44	5	571
Surface Water	2	1	1	5	1	10

[1] NPCG (Norman, Peter, Cooper, Ginger islands)

References

[1] J. J. Ewel and J. L. Whitmore, "The Ecological life zones of Puerto Rico and the U.S. Virgin Islands," Forest Service research paper ITF-018, Institute of Tropical Forestry, Rio Piedras, Puerto Rico, pp. 72 (1973).

[2] The University of the Virgin Islands, Conservation Data Center, "Rapid Ecological Assessment," St. Thomas, VI. U.S.A., pp. 56 (2000).

[3] J. S Beard, "The natural vegetation of the Windward and Leeward Islands," *Geogr. Rev.***4**, pp 350 (1949).

[4] T. Kennaway and E. H. Helmer, "The forest types and ages cleared for land development in Puerto Rico", *GIScience and Remote Sensing***44** (4), 356-382 (2007) [doi:10.2747/1548-1603.44.4.356].

[5] E. H. Helmer, T. Kennaway, D. Pedreros, M. Clark, H. Marcano, L. Tieszen, T. Ruzycki, S. Schill and C. M. S. Carrington, "Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery," *Caribb. J. Sci.* **In Press,** (2008).

[6] E. H. Helmer and B. Ruefenacht, "A comparison of radiometric normalization methods when filling cloud gaps in Landsat imagery," *Can. J. Remote Sensing***33**(4), 325-340 (2007).

[7] M. A. Lefsky, W. B. Cohen, G. G. Parker, and D. J. Harding, "Lidar remote sensing for ecosystem studies," *Bioscience* **52**(1), 19-30 (2002) [doi:10.1641/0006-3568(2002)052[0019:LRSFES]2.0.CO;2].

[8] R. O. Woodbury and P. L. Weaver, "The vegetation of St. John and Hassel Island: U. S. Virgin Islands," U.S. DOI National Park Service, Georgia (1997).

[9] J. Rogozinski, *A brief history of the Caribbean. From the Arawak and Carib to the present, (revised edition)*, Penguin Group, New York, pp. 30 (2000).

[10] P. L. Weaver, "Estate Thomas Experimental Forest: St. Criox, U.S. Virgin Islands: Research history and potential', General technical Report IITF-30, USDA Forest Service International Institute of Tropical Forestry, San Juan, Puerto Rico, pp. 62 (2006).

[11] P. L. Weaver, "A summary of 20 years of forest monitoring in Cinnamon Bay watershed, St. John, U.S. Virgin Islands," General Technical Report IITF-34, USDA Forest Service International Institute of Tropical Forestry, San Juan, Puerto Rico pp. 47 (2006).

[12] S. N. Oswalt, T. J. Brandeis, and B. P. Dimick, "Phytosociology of vascular plants on an international biosphere reserve: Virgin Islands National Park, St. John, US Virgin Islands," *Caribb J. Sci.* **42**(1), 53-66 (2006).

[13] E. H. Helmer, "Forest conservation and land development in Puerto Rico," *Landscape Ecol.* **19**(1), 29-40 (2004) [doi:10.1023/B:LAND.0000018364.68514.fb].

[14] T. J. Brandeis and S. N. Oswalt, The status of the U.S. Virgin Islands' Forests, 2004, Resource Bulletin SRS-122, USDA Forest Service Southern Research Station, Asheville, NC (2007).

[15] P. G. Murphy, and A. Lugo, "Ecology of tropical dry forest", *Annu. Rev. Ecol. Syst.***17**, 67-88 (1986).

[16] M. A. Friedl, C. E. Brodley A. H. Strahler, "Maximizing land cover classification accuracies produced by decision trees at continental to global scales," *IEEE T. Geosci. Remote* **37**(2), 969-977 (1999).

[17] M. B. Carreiras, M. C. Pereira, and E. Shimabukuro, "Land-cover mapping in the Brazilian Amazon using SPOT-4 vegetation data and machine learning classification methods," *Photogramm. Eng. Remote Sensing* **72**(8), 1449-1464 (2006).

[18] M. A. Lefsky, W. B. Cohen, S. A. Acker, G. G. Parker, T. A. Spies, and D. J. Harding, "Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir Western Hemlock forests," *Remote Sensing of Environment* **70**(3), 339-361 (1999) [doi:10.1016/S0034-4257(99)00052-8].

[19] J. E. Means, S. A. Acker, D. J. Harding, J. B. Blair, M. A. Lefsky, W. B. Cohen, M. E. Harmon, and W. A. McKee, "Use of large-footprint scanning lidar to estimate forest stand characteristics in the western Cascades of Oregon," *Remote Sens. Environ.* **67**(3), 298-308 (1999) [doi:10.1016/S0034-4257(98)00091-1].

[20] V. Thomas, P. Treitz, J. H. McCaughey and I. Morrison, "Mapping stand-level boreal forest biophysical variables for a mixedwood boreal forest using lidar: an examination of scanning density," Can. J. For. Res. **36**(1), 34-47 (2006) [doi:10.1139/x05-230].

[21] E. Næsset and T. Okland, "Estimating tree height and tree crown properties using airborne scanning laser in a boreal nature reserve," *Remote Sens. Environ.* **79**(1), 105-115 (2002).

[22] S. C. Popescu, R. H. Wynee, and R. F. Nelson, "Estimating plot-level tree heights with lidar: local filtering with a canopy-height based variable window size," *Comput. Electron Agr.* **37**(1), 71-95 (2002) [doi:10.1016/S0168-1699(02)00121-7].

[23] K. S. Lim and P. M. Treitz, "Estimation of Above ground Forest Biomass from airborne Discrete Return Laser Scanner Data Using Canopy-based Quantile Estimators," *Scand J For Res.* **19**(6), 558-570 (2004) [doi: 10.1080/02827580410019490].

[24] G. Patenaude, R. A. Hill, R. Milne, D. L. A. Gaveau, B. B. J. Briggs and, T. P. Dawson, "Quantifying forest above ground carbon content using LiDAR remote sensing," *Remote Sens. Environ.* **93**(3), 368-380 (2004) [doi:10.1016/j.rse.2004.07.016].

[25] S. C. Popescu, R. H. Wynne, and R. F. Nelson, "Measuring individual tree crown diameter with lidar and assessing its influence on estimating forest volume and biomass," *Caribb J. Sci.* **29**(5), 564-577 (2003).

[26] F. Morsdorf, E. Meier, B. Kötx, K. I. Itten, M. Bobbertin, and B. Allgöwer, "LIDAR-based geometric reconstruction of boreal type forest stands at single tree level for forest and wildland fire management," *Remote Sens. Environ.* **92**(3), 353-362 (2004) [doi:10.1016/j.rse.2004.05.013].

[27] N. Skowronski, K. Clark, R. Nelson, J. Hom, and M. Patterson, "Remotely sensed measurements of forest structure and fuel loads in the Pinelands of New Jersey," *Remote Sens. Environ.* **108**(2), 123-129 (2007) [doi:10.1016/j.rse.2006.09.032].

[28] R. Nelson, "Modeling Forest Canopy Heights: The Effects of Canopy Shape," *Remote Sens. Environ.* **60**(3), 311-326 (1997) [doi:10.1016/S0034-4257(96)00213-1].

[29] USDA Forest Service, "Forest Stewardship program (Puerto Rico and Virgin Islands region)," U. S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Puerto Rico (2007).

[30] L. R. Holdridge, *Life zone ecology, (Revised edition)*, Tropical Science Center, San José, Costa Rica, pp. 206 (1967).

[31] E. H. Helmer and B. Ruefenacht, "Cloud-free satellite image mosaics with regression trees and histogram matching," Photogramm. Eng. Remote Sensing **71**(9), 1079-1089 (2005).

[32] ERDAS, Inc, "Leica Geosystems ERDAS Imagine version 8.7," 2007, http://gi.leica-geosystems.com/LGISub1x20x0.aspx, (10 November 2007).

[33] L. Fox, M Garrett, R. Heasty, and E. Torres, "Classifying wildlife habitat with pan-sharpened Landsat 7 imagery," *ISPRS Commission, I/FIEOS 2002 Conference Proceedings*, pp. 11 (2002).

[34] T. M. Lillesand, R. W. Kiefer, and J. W. Chipman, *Remote sensing and image interpretation (Fifth edition)*, John Wiley and Sons, New York, pp. 784 (2004).

[35] A. H. Strahler, "Stratification of natural vegetation for forest and rangeland inventory using Landsat imagery and collateral data," Int. J. Remote Sens. **2**(1), 15-41 (1981) [doi:10.1080/01431168108948338].

[36] A. K. Skidmore, "An expert system classifies eucalypt forest types using thematic mapper data and a digital terrain model," Photogramm. Eng. Remote Sensing **55**(10), 449-1464 (1989).

[37] D. M. Gesch, Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler, "The National Elevation Dataset", Photogramm. Eng. Remote Sensing **68**(1), 5-11 (2002).

[38] T. G. Farr and M. Kobrick, "Shuttle Radar Topography Mission produces a wealth of data," Amer. Geophys. Union Eos **81**, 583-585 (2000).

[39] United States Geological Survey, 1:24,000 digital line graphs, Reston, Virginia, 2007, http://edc.usgs.gov/products/map/dlg.html, (September 20, 2007).

[40] M. A. Friedl and C. E. Brodley, "Decision tree classification of land cover from remotely sensed data," Remote Sens. Environ. **61**(3), 399-409 (1997) [doi:10.1016/S0034-4257(97)00049-7].

[41] M. Fiorella and W. J. Ripple, "Determining successional stage of temperate coniferous forests with Landsat satellite data," Photogramm. Eng. Remote Sensing **59**(2), 239-246 (1993).

[42] E. H. Helmer, W. B. Cohen, and S. Brown, "Mapping montane forest successional stage and land use with multi-date Landsat imagery," International Int. J. Remote Sens. **21**(11), 2163-2183 (2000) [doi:10.1080/01431160050029495].

[43] R. A. Schowengerdt, *Remote sensing: models and methods for image processing (Second edition),* Elsevier, New York, pp. 522 (1997).

[44] E. H. Helmer, O. Ramos, T. d. M. Lopez, M. Quiñones, and W. Diaz, "Mapping forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot," Caribb J. Sci. **38**(3), 165-183 (2002).

[45] A. Areces-Mallea, A. S. Weakley, X. Li, R. G. Sayre, J. D. Parrish, C. V. Tipton, and T. Boucher, "A guide to Caribbean vegetation types: classification systems and descriptions," The Nature Conservancy, Washington, D.C. (1999).

[46] FGDC, "National Vegetation Classification Standard," Federal Geographic Data Committee, Vegetation Subcommittee. FGDC-STD-005, U.S. Geological Survey, Reston, Virginia (1997).

[47] RuleQuest Research, Data Mining Tools See5 and C5.0, 2007 http://www.rulequest.com/see5.htm, (November 20, 2007).

[48] J. R. Quinlan, *C4.5: programs for machine leaning*, Morgan Kaufmann, California (1993).

[49] R. G. Congalton, "A review of assessing the accuracy of classifications of remotely sensed data," Remote Sens. Environ. **37**(1), 35-46 (1991) [doi:10.1016/0034-4257(91)90048-B].

[50] S. V. Stehman and R. L. Czaplewski, "Design and analysis for thematic map accuracy assessment: fundamental principles," Remote Sens. Environ. **64**(3), 331-334 (1998) [doi:10.1016/S0034-4257(98)00010-8].

[51] 3001 Inc., Puerto Rico Ground Control Report, Contract No: DACW43-03-D-0504 (2004).

[52] Q. Chen, "Airborne lidar data processing and information extraction," Photogramm. Eng. Remote Sensing **73**, 109-112 (2007).

[53] K. Zhang, S. Chen, D. Whitman, M. Shyu, J. Yan, and C. Zhang, "A progressive morphological filter for removing nonground measurements from airborne lidar data," IEEE T. Geosci. Remote **41**(4), 872-882 (2003) [10.1109/TGRS.2003.810682].

[54] Q. Chen, P. Gong, D. Baldocchi, and G. Xie, "Filtering airborne laser scanning data with morphological methods", Photogramm. Eng. Remote Sensing **73**(2), 175-185 (2007).

[55] M. A. Lefsky, Interactive Data Language (IDL) algorithm for Lidar point cloud data, Colorado State University, Fort Collins, Colorado (2007).

[56] M. A. Lefsky, "Application of Lidar Remote sensing to the estimation of forest canopy and stand structure", PhD Thesis,University of Virginia (1997).

[57] T. J. Brandeis and S. N. Oswalt, "The status of U.S. Virgin Islands' forests, 2004," Resource Bulletin SRS-122, USDA Forest Service Southern Research Station, Ashville, NC (2007).

[58] USDA Forest Service, "Field Procedures for Puerto Rico and the Virgin Islands, Supplement C to SRS Regional Manual 1.56", USDA Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit, Knoxville, TN, 2002, http://srsfia2.fs.fed.us/data_acquisition/manual.shtml (June 25, 2008).

[59] D. Hatfield, Slope Position AML (ARC/INFO 7.2.1). USDA Forest Service, Pacific Northwest Region, Portland, Oregon (1999).

[60] B. Ruefenacht, M. V. Finco, M. D. Nelson, R. Czaplewski, E. H. Helmer, J. A. Blackard, G. R. Holden, A. J. Lister, D. Salajanu, D. Weyermann, K. Winterberger, "Conterminous U.S. and Alaska forest type mapping using forest inventory and analysis data," Photogramm. Eng. Remote Sensing **In Press**, (2008).

[61] SAS Institute Inc., "JMP Statistical Software", 2007, http://www.jmp.com.

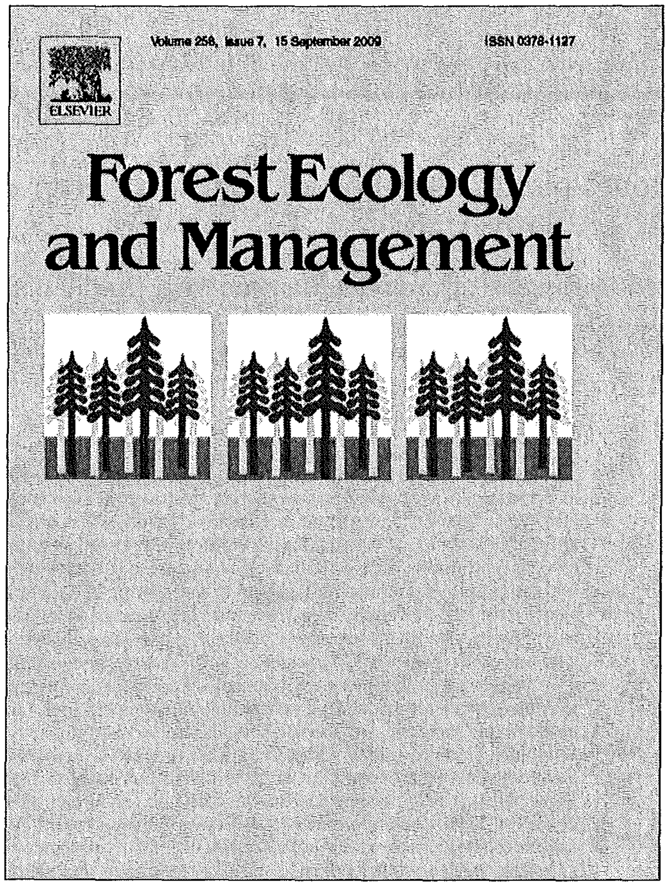
[62] P. L. Weaver, "Forest productivity of the Cinnamon Bay watershed, St. John, U.S. Virgin Islands," Caribb. J.Sci. **32**, 89-98 (1996).

[63] D. F. Whigham, I. Olmsted, E. C. Cano, and M. E. Harmon, "The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the Northeastern Yucatan Peninsula," Biotropica **23**(4), 434-441 (2006) [doi:10.2307/2388263].

[64] P. G. Murphy and A. E. Lugo, *Dry Forests of Central America and the Caribbean*, pp. 9-34 in S.H. Bullock, H.A. Mooney and E. Medina, *seasonally dry tropical forests*, Cambridge University Press, New York, NY (1995).

[65] A. Wehr, and U. Lohr, "Airborne laser scanning-an introduction and overview," ISPRS J.Photogramm. **54**(2-3), 68-82(1999) [doi:10.1016/S0924-2716(99)00011-8].

[66] R. Cunningham, D. Gisclair, and J. Craig, "The Louisiana Statewide LIDAR Project," (n.d.), ftp://ftp-fc.sc.egov.usda.gov/NCGC/products/elevation/la-lidar-project.pdf, (September 20, 2007).



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Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands

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ABSTRACT

Environmental and past land use controls on tree species assemblages on the Commonwealth of Puerto Rico and the U.S. Virgin Islands were characterized to determine whether biophysical factors or land-use history has been more important in determining the species composition of secondary tropical forests after large-scale forest clearing for agriculture, widespread species introduction, and landscape-scale forest fragmentation. Post-deforestation, secondary forest assemblages are comprehensively described, both as broad general assemblages and island-specific variations by calculating species importance values from forest inventory data. Hierarchical clustering and indicator species analysis defined species assemblages, and then correlations between species assemblages and environmental variables were explored with non-metric multidimensional scaling, analysis of variance and χ^2 testing. These assemblages are arrayed along environmental gradients of decreasing spring moisture stress, decreasing maximum temperatures, and increasing minimum temperatures. Land-use history is not as important to determining variation in species composition across climatic zones, although several species assemblages are associated with certain geology types or land-use histories. Naturalized tree species are prominent in these secondary forests and contribute to the formation of some novel assemblages, but native late and early successional species also colonize former agricultural land, all influenced by the degree of disturbance. We conclude that environmental factors have an overarching effect on forest species composition across the broader range of climatic, geologic and topographic conditions and larger geographic scales, while land-use history influences subtropical secondary forest species assemblages within a specific climatic zone or set of relatively narrow environmental conditions.

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1. Introduction

In many tropical regions, clearing of old-growth tropical forests for agriculture has accelerated over the last decade. Deforestation for industrial-scale agriculture clears larger areas faster than the forest clearing for small-scale or subsistence agriculture that dominated in earlier decades. In some countries, however, secondary tropical forests are recovering on much of the land previously cleared for agriculture (Kauppi et al., 2006), including several countries in the Caribbean, which is the location of this study (Helmer et al., 2008). These secondary forests provide our best opportunities to answer questions about the relative influences of land-use history *vs.* climate and other biophysical influences on secondary forest species composition. Yet understanding the relative importance of these factors sheds light on secondary forest successional processes, biodiversity maintenance, and introduced species dynamics across the tropics where secondary forests are expected to cover increasingly large areas.

The forests of Puerto Rico and the U.S. Virgin Islands, the subject of this research, have undergone near complete clearing since European colonization began in the early 1500s. Since the 1950s, there has been large-scale agricultural abandonment and forest recovery. In some instances, the secondary forests that have emerged are novel species assemblages, distinct from the pre-colonization forests due to the widespread introduction and naturalization of many tree species (Aide et al., 1996; Zimmerman et al., 2000; Chinea and Helmer, 2003; Lugo and Helmer, 2004). We need to better understand how these emerging secondary forests have formed if we are to manage them for the sustainable delivery of ecosystem services (Hobbs et al., 2006).

Most previous studies of the influence of land-use history on secondary forests communities in Puerto Rico are limited to samples selected along land-use gradients within small landscapes that encompass only one climatic zone and substrate type (García-Montiel and Scatena, 1994; Rivera and Aide, 1998;

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Pascarella et al., 2000; Thompson et al., 2002, 2007; Molina and Lugo, 2006). These studies find that past land use has an overriding impact on secondary forest species composition. Though we know from this previous work that land-use history can strongly influence the species composition of secondary tropical forests, we do not know whether previous land use contributes significantly to variation in species composition across large landscapes. No studies characterize the relative influences of land-use history *vs.* biophysical variables on secondary forest communities over environmental gradients that, for example, include both dry and wet climatic zones. A systematic sample of secondary forest communities across two humid climatic zones and two main geologic classes of Puerto Rico, however, concludes that previous land-use interacts with climate and substrate to determine tree species composition (Chinea and Helmer, 2003).

In this study, we test a suite of environmental and land-use history variables to learn which factors contribute most to explaining variation in the species composition of secondary tropical forests across a more diverse environmental gradient than previous work. In addition, instead of selecting sites along gradients designed to test whether previous land use is important, we use a systematic sample based on forest inventory data. With a systematic sample design, the forest stand data quantitatively represent the actual variation in species composition that exists across a landscape. Consequently, this sample design should help reveal what will most influence tropical forest communities when secondary forests recover after large-scale clearing, agricultural use and abandonment. We expect that climate will explain much of the variation in forest community structure in the systematic sample of forest stands across a steep environmental gradient, but that land-use history will still be important. To test this hypothesis, the objectives of this study are to (1) describe forest communities of Puerto Rico and the U.S. Virgin Islands that have developed after land-use histories characterized by deforestation for agriculture, abandonment, and subsequent forest regeneration; (2) determine which environmental and land-use history factors best correlate with the gradients that define these forest assemblages; and (3) test whether forest assemblage is related to land use as mapped in 1951, 1977, 1991 and 2000.

2. Methods

We used hierarchical clustering and indicator species analysis to define species assemblages in data from systematically placed forest inventory plots across Puerto Rico and the U.S. Virgin Islands. Differences between assemblage trees per hectare (TPH), basal area per hectare (BAH), live aboveground biomass per hectare (AGBH), and average canopy height (HT) were tested with analysis of variance (ANOVA). We explored the correlations between species assemblages and environmental variables with non-metric multidimensional scaling (NMS), and further explored assemblage distribution across land cover types over 4 time periods; 1951, 1977, 1991 and 2000 on mainland Puerto Rico with χ^2 testing.

2.1. Study area

The Commonwealth of Puerto Rico consists of the islands of Puerto Rico, Vieques, Culebra (the latter two sometimes referred to as the Spanish Virgin Islands), and a number of smaller islands centered on 18°15′N by 66°30′W (Fig. 1). The U.S. Virgin Islands, an unincorporated territory of the United States, are made up of St. Croix, St. John, St. Thomas and many smaller islands centered on the geographic coordinates of 18°20′N by 64°50′W (Fig. 1).

Extensive deforestation for agriculture began on Puerto Rico with European colonization and continued until the early 1950s when it was estimated that the island was 96% deforested (Wadsworth, 1950; Birdsey and Weaver, 1982). Widespread abandonment of agricultural land due to socioeconomic changes has allowed forest recovery (Thomlinson et al., 1996; López et al., 2001; Helmer, 2004; Kennaway and Helmer, 2007; Helmer et al., 2008) to such an extent that forest cover had reached 32% by 1980 (Birdsey and Weaver, 1982) and 57% by 2003 (Brandeis et al., 2007). The forests of the U.S. Virgin Islands also experienced a

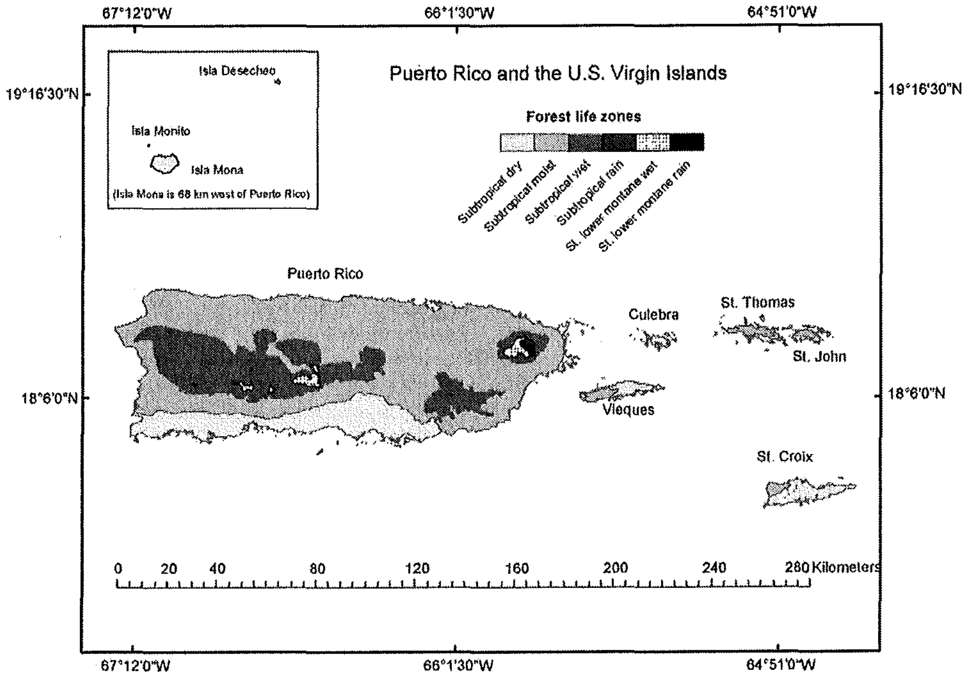

Fig. 1. Map of Puerto Rico and the U.S. Virgin Islands with forest life zones derived from Ewel and Whitmore (1973).

colonial period of deforestation for export agriculture followed by forest recovery (Weaver, 2006a,b). Forest cover had increased to 68% in 1994, but decreased to 61% by 2004 from other development pressures (Brandeis and Oswalt, 2007).

High species endemism, high physiographic complexity over relatively small areas, and a natural disturbance regime of hurricanes, and less frequently drought, created diverse forest communities (Lugo et al., 2000; Myers et al., 2000). The addition of anthropogenic disturbance and naturalized species further increased the complexity of Caribbean forest successional processes and the resulting tree species assemblages (Lugo and Helmer, 2004; Lugo and Brandeis, 2005; Brandeis, 2006).

Many researchers recognize the relationships between the rugged topography, climatic gradients, and forest vegetation of Puerto Rico. Forest vegetation reflects the marked environmental and climatic gradients resulting from the interaction between Trade Winds and abrupt elevation changes. Birdsey and Weaver (1982), Ewel and Whitmore (1973), and Little and Wadsworth (1989) give excellent descriptions of the forest associations found on Puerto Rico, though they focus on mature forest communities (Ewel and Whitmore, 1973). Holdridge life zones are commonly used to describe vegetation zones in these islands, and they have been the basis for reporting forest categories in the previous forest inventories. These categories will also be used here to group forest assemblages.

Subtropical dry forest conditions predominate at lower elevations along coasts and in southwest Puerto Rico, over most of Vieques, all of Culebra, and most of the U.S. Virgin Islands (Ewel and Whitmore, 1973; Birdsey and Weaver, 1982; Brandeis et al., 2007). Subtropical moist forest occurs at higher elevations on Vieques, St. Croix, St. John and St. Thomas where higher elevations cause the orographic cooling of moisture carried on the Trade Winds, increasing precipitation. Subtropical wet forests and subtropical rain forests occur at the higher elevations found only on mainland Puerto Rico. Additionally, subtropical lower montane wet forests and subtropical lower montane rain forests are found in the Luquillo Mountains of Puerto Rico.

2.2. Forest inventory

Field crews installed 369 permanent forest inventory plots spread across mainland Puerto Rico, Vieques, Culebra, St. Croix, St. John and St. Thomas. Field crews visited all sampling points and installed plots on mainland Puerto Rico in the months of January through July in 2001–2003. Sampling points on Vieques, Culebra, St. Croix, St. John and St. Thomas were visited from February to October in 2004.

Generally, plots were equally spaced on a systematic sampling grid (see McCollum, 2001; Brandeis, 2003 for details). While most inventory plots were systematically placed in an un-biased sample, 24 plots were added as a stratified sample in subtropical lower montane forests, forests on ultramafic (serpentine) substrate, and more mature subtropical dry forests on mainland Puerto Rico. In addition, sampling intensity on St. John was double that of the other Virgin Islands to benefit management of the Virgin Islands National Park (Oswalt et al., 2006). Plots could not be installed on substantial portions of eastern Vieques because of past U.S. Navy activity.

The permanent plots consisted of a four-subplot cluster. Each subplot in the cluster has a 7.3 m radius, so total sampled area is 0.067 ha per permanent plot for trees with diameter at breast height (d.b.h., measured at 1.37 m) $\geq$12.5 cm. Trees with d.b.h. $\geq$ 2.5 cm were measured in a 2.1 m radius microplot nested within each subplot. Detailed information on plot location, installation, and monumentation, and site descriptions, tree measurement, tree damage description, and other data collected at each forested plot can be found in the USDA Forest Service's Forest Inventory and Analysis, Southern Research Station Field Guide, Field Procedures for Puerto Rico and the Virgin Islands (USDA Forest Service, 2002) or in Bechtold and Scott (2005).

Species nomenclature was based on the USDA-NRCS PLANTS database (USDA Natural Resource Conservation Service, 2009), with supplemental reference to Little and Wadsworth (1989) and Little et al. (1974). Molina and Alemañy (1997) was used as an additional reference to determine which tree species were native or introduced to the U.S. Virgin Islands. The species relative importance value (IV) was calculated for each inventory plot by taking the average of relative dominance (each species' basal area (BA) divided by the total BA) and relative density (each species' trees per hectare divided by total trees per hectare), multiplied by 100 (Curtis and McIntosh, 1951; Whittaker, 1975).

2.3. Clustering, indicator species analyses and assemblage structural characteristics

The full primary species matrix consisted of species' IV by inventory plot for 369 inventory plots and 328 species. Hierarchical agglomerative cluster analysis was performed using a Flexible Beta linkage method (beta = −0.25) and Sørensen distance measure (PC-Ord Version 5.0, McCune and Mefford, 1999). Preliminary analyses of the full primary species matrix revealed outlying points that exceeded 2 standard deviations in Euclidean distance which were then deleted from the matrices. Plots that fell in mangrove forest were removed from the analysis because the inventory had few plots in mangrove and the composition of mangrove forest is already well defined. Preliminary ordinations showed stronger correlations between species assemblages and environmental variables after removal of rare species. Relatively rare species that were found in less than 5 plots were removed from the primary matrix to reduce "noise" in the data and strengthen the extraction of pattern from the data (McCune and Grace, 2002). After all of these reductions, final cluster and indicator species analyses were run on a data set consisting of all islands combined, and then on the data split into two data sets; the 270 plots and 92 species on mainland Puerto Rico and the 89 plots and 45 species on Vieques, Culebra and the U.S. Virgin Islands, which henceforth will be referred to simply as the Virgin Islands. Splitting the data allowed us to show both the broadly defined, general species assemblages that span multiple islands and the unique variations created by local environmental factors and differing land-use histories on the Virgin Islands that might otherwise be lost within the larger, mainland Puerto Rico dominated dataset.

DuFrêne and Legendre (1997) indicator species analysis was used both to ascertain which species defined the clusters and to help guide the selection of an optimum number of clusters as per the description given in McCune and Grace (2002). The final decision on the optimal number of ecologically meaningful clusters was based the methods outlined in McCune and Grace (2002), the indicator species analysis results, field experience, literature review and mapping in a GIS to better visualize their spatial distribution.

Mean structural characteristics (quadratic mean diameter (QMD), TPH, BAH, AGBH, HT) were calculated for each assemblage identified by the cluster analyses. Assemblage QMD (d.b.h. in centimeters), TPH (number of stems per hectare), BAH (m^2/ha) and AGBH (oven-dry Mg per hectare, including foliage) are for all stems with d.b.h. $\geq$ 12.5 cm. Methods and allometric equations used for estimating AGBH are described in Brandeis et al. (2007). Canopy height is the average height (m) for all trees that were considered dominant or co-dominants in the stand. Assemblage mean values were estimated and compared with SAS using the General Linear Model procedure (PROC GLM) for uneven sample sizes and Least Squares Means pairwise comparisons (Freund and Littel, 1981; SAS Institute, 2004).

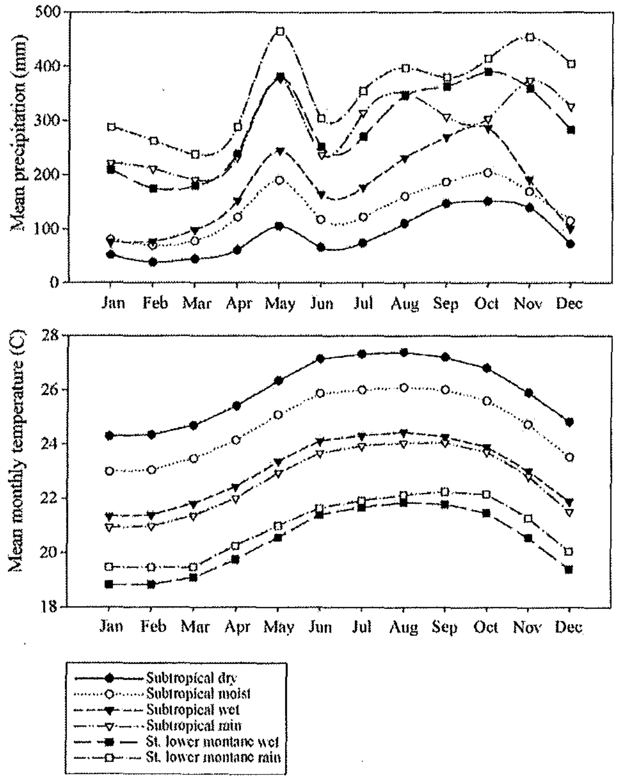

Fig. 2. Thirty-year average monthly precipitation (mm) and average monthly temperature (°C) on Puerto Rico and the U.S. Virgin Islands by Holdridge life zone.

2.4. Non-metric multidimensional scaling and assemblage frequency distributions

A secondary environmental matrix was filled with continuous and categorical variables collected at the plot by field crews or extracted from GIS coverages. We used plot center coordinates to extract the environmental attributes of each plot from digital maps of climate, topography, geology, historical land-cover and nearest distance to a coastline. Climate data included 30-year average monthly and annual precipitation as well as minimum, maximum and mean temperatures (Fig. 2) for both Puerto Rico (Daly et al., 2003) and the Virgin Islands (Fig. 3).

Topographic variables included elevation, percent slope, aspect, cosine aspect, degrees from North, and slope position (Hatfield, 1999), and they were extracted from 30-m digital elevation models (Gesch et al., 2002). Land-cover data included generalized land cover in 1951, 1977, 1991 and 2000, as well as forest age class derived from the four land-cover maps (Kennaway and Helmer, 2007). Generalized geology came from the map of Krushensky (1995) for Puerto Rico, and from a hard copy map (Garrison et al., 1972) digitized by Colorado State University and later edited.

To better represent growing conditions at each plot, annual and seasonal moisture stress indices were calculated as in Ohmann and Spies (1998). The annual moisture stress was represented by dividing the average annual temperature by the average annual precipitation. Seasonal moisture stress indices for spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February) were also calculated by dividing the average monthly temperature for the three-month period by the average monthly precipitation for that period.

Non-metric multidimensional scaling was run with the Sørensen distance measures (PC-Ord Version 5.0, McCune and Mefford, 1999). Preliminary NMS runs (using the autopilot, thorough mode) established the best dimensionality and starting coordinates (McCune and Mefford, 1999) for the final NMS runs.

Frequency distribution tables of assemblage occurrence in different life zones, age classes, and land cover classes were generated with frequency procedure (PROC FREQ) in the Statistical Analysis System (SAS, Version 9.1) package (SAS Institute, 2004). Chi-Squared (χ^2) and Cochrane–Mantel–Haenszel tests were employed to look for significant (α-level = 0.05) differences in the distribution of each assemblage across life zones, geologic substrates, and 3 past land uses (specifically, that last land use

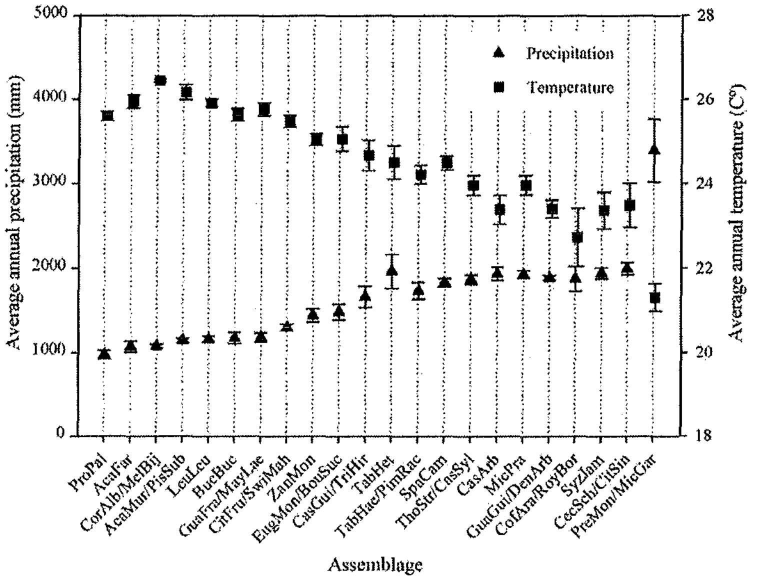

Fig. 3. Average annual precipitation (mm) and average annual temperature (°C) with standard errors of the mean at forest inventory plots where each tree species assemblage was encountered. Assemblages are the result of hierarchical clustering on the combined data from Puerto Rico and the U.S. Virgin Islands.

before reversion to forest). Plots were grouped into 5 life zone/geologic substrate categories to aid in interpretation, as was done in Helmer et al. (2002). These groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical dry–moist on ultramafic (Dry, Moist/Ultra), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moist–wet on limestone (Moist, Wet/Lime), subtropical wet on alluvial, volcanic and sedimentary (Wet/AVS), subtropical lower montane on alluvial, volcanic and sedimentary (LM/AVS), and subtropical wet–subtropical lower montane on ultramafic (Wet, LM/Ultra).

3. Results

3.1. Tree species assemblages and their characteristics

Clustering resulted in 22 tree species assemblages in the combined, all-islands dataset (Table 1); 14 assemblages from mainland Puerto Rico data (Table 2); and 8 assemblages from the Virgin Islands data (Table 3). (Assemblage names were taken from the first 3 letters of the 2 most significant indicator species ($P < 0.05$), or single significant indicatory species if only one was present.) The assemblages found in clustering the combined data from all islands are distributed along gradients of increasing average annual precipitation and decreasing average annual temperature (Fig. 2) that correspond to increases in elevation. Assemblages are ordered in the tables by decreasing mean annual moisture stress at the inventory plots where they were found, and origin (native to the islands or introduced post-European colonization) is included for each species. The mean structural characteristics (QMD, TPH, BA, AGB, and HT) for assemblages found across all the islands, on mainland Puerto Rico and in the Virgin Islands (Table 4) show the wide range in forest structure.

3.2. Environmental correlations with ordination axes

Scree plots and stress statistics indicated that a three-dimensional solution best fit the combined and separate data sets for the NMS ordination. After ranking by R^2 of the first ten most significant environmental variables and tree species correlated with each of the 3 ordination axes, we found that only environmental variables were significant, specifically the climate variables (Tables 5–7).

Ordination of data from all the islands combined resulted in a cumulative R^2 value of 0.434 for 3 axes. All-islands ordination axis 1 was negatively correlated with spring and annual moisture stress (Table 5), and positively correlated with mean monthly precipitation in April, distance from the coast, and May precipitation. Tree species that were negatively correlated with this axis included *Leucaena leucocephala* (Lam.) de Wit, *Acacia farnesiana* (L.) Willd., and *P. pallida*, species found in lower elevation, degraded areas in subtropical dry and moist forest zones. Species that were positively correlated with these axes included *Guarea guidonia* (L.) Sleumer and *Casearia guianensis* Aubl., which occur in subtropical moist and subtropical wet forest zones. All-islands axis 2 showed positive correlations with minimum monthly temperature in March, January and November. Positively correlated species included *Bursera simaruba* (L.) Sarg. and *Tabebuia heterophylla* (DC.) Britt., species found in both subtropical moist and subtropical dry forest. At the other end of the axis were higher elevation, subtropical wet species such as *G. guidonia* and *Cecropia schreberiana* Miq. All-islands axis 3 was negatively correlated with mean maximum temperatures in September and June, and it positively correlated with elevation. The species *L. leucocephala* and *Spathodea campanulata* Beauv. were negatively correlated with axis 3 while

Table 1
Tree species assemblages for all islands combined, with importance value (IV), indicator species P (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Assemblage	Species	IV	P	Origin
ProPal	**Prosopis pallida**	88.5	0.001	I
	Acacia macracantha	11.6	0.108	I
	Cordia laevigata	6.2	0.326	N
AcaMur/PisSub	**Acacia muricata**	81.8	0.001	N
	Pisonia subcordata	62.2	0.001	N
	Eugenia cordata	53.8	0.001	N
	Capparis cynophallophora	47.9	0.001	N
	Myrciaria floribunda	45.6	0.001	N
	Amyris elemifera	19.1	0.013	N
	Cassine xylocarpa	10.8	0.087	N
	Capparis hastata	8.3	0.209	N
	Pilosocereus royenii	5.1	0.465	N
AcaFar	**Acacia farnesiana**	87.0	0.001	I
	Albizia lebbeck	3.8	0.665	I
LeuLeu	**Leucaena leucocephala**	58.9	0.001	N
	Samanea saman	3.7	0.642	I
CorAlb/MelBij	**Cordia alba**	91.1	0.001	N
	Melicoccus bijugatus	24.8	0.010	I
	Croton astroites	15.2	0.029	N
	Adelia ricinella	13.8	0.071	N
	Eugenia rhombea	12.8	0.070	N
	Tecoma stans	9.3	0.188	N
	Krugiodendron ferreum	8.9	0.152	N
EugMon/BouSucc	**Eugenia monticola**	67.7	0.001	N
	Bourreria succulenta	23.2	0.005	N
	Sabinea florida	21.3	0.005	N
	Guettarda scabra	16.4	0.018	N
	Randia aculeata	13.2	0.040	N
	Coccothrinax alta	4.3	0.556	N
	Ocotea floribunda	4.1	0.601	N
	Casearia decandra	3.8	0.620	N
	Tabebuia heterophylla	65.4	0.001	N
	Coccoloba diversifolia	9.7	0.116	N
	Cordia sulcata	5.1	0.482	N
	Casearia guianensis	56.4	0.001	N
	Trichilia hirta	20.2	0.021	N
	Guazuma ulmifolia	19.3	0.009	N
	Andira inermis	12.5	0.044	N
	Myrcia splendens	8.1	0.159	N
	Cupania americana	4.8	0.496	N
	Thouinia striata	41.1	0.002	N
	Casearia sylvestris	30.5	0.003	N
	Ficus citrifolia	13.4	0.055	N
	Myrsine coriacea	9.8	0.145	N
	Eugenia biflora	9.5	0.115	N
	Tetrazygia elaeagnoides	8.6	0.181	N
	Trichilia pallida	3.5	0.684	N
	Delonix regia	3.4	0.686	I
	Casearia arborea	21.9	0.010	N
	Psidium guajava	13.0	0.081	N
	Ocotea leucoxylon	8.8	0.119	N
	Ormosia krugii	8.8	0.218	N
	Trema micranthum	6.7	0.328	N
	Hymenaea courbaril	6.0	0.376	N
	Buchenavia tetraphylla	4.4	0.503	N
	Quararibea turbinata	2.4	0.840	N
	Coffea arabica	91.6	0.001	I
	Roystonea borinquena	14.5	0.025	N
	Homalium racemosum	13.7	0.044	N
	Petitia domingensis	8.9	0.169	N
	Miconia prasina	11	0.12	N
	Piper amalago	3.3	0.733	N
GuaFra/MayLae	**Guapira fragrans**	58.8	0.001	N
	Maytenus laevigata	48.2	0.001	N
	Cordia alliodora	29.5	0.005	N
	Bursera simaruba	22.4	0.004	N

Table 1 (*Continued*)

Assemblage	Species	IV	P	Origin
	Capparis indica	20.2	0.040	N
	Ocotea coriacea	13.0	0.069	N
	Chionanthus compactus	12.4	0.077	N
	Faramea occidentalis	9.5	0.118	N
	Capparis baducca	6.4	0.316	N
	Chrysophyllum pauciflorum	2.5	0.865	N
ZanMon	**Zanthoxylum monophyllum**	22.0	0.014	N
	Exostema caribaeum	6.6	0.264	N
	Ardisia obovata	6.3	0.299	N
	Senna siamea	6.3	0.345	I
	Pictetia aculeata	5.0	0.470	N
	Cinnamomum elongatum	4.2	0.599	N
CitFru/SwiMah	**Citharexylum fruticosum**	71.2	0.001	N
	Swietenia mahagoni	19.0	0.006	I
	Ziziphus mauritiana	9.8	0.157	I
	Tamarindus indica	5.1	0.468	I
BucBuc	**Bucida buceras**	13.8	0.033	N
	Pithecellobium dulce	12.1	0.099	I
	Albizia procera	7.7	0.201	I
SpaCam	**Spathodea campanulata**	60.9	0.001	I
	Thespesia grandiflora	5.8	0.389	N
	Terminalia catappa	2.4	0.844	I
	Erythroxylum rotundifolium	1.6	0.972	N
TabHae/PimRac	**Tabebuia haemantha**	52.3	0.001	N
	Pimenta racemosa	45.9	0.002	N
	Neolaugeria resinosa	42.8	0.001	N
	Clusia rosea	23.9	0.007	N
	Licaria parvifolia	10.7	0.078	N
	Annona muricata	9.3	0.177	N
	Ocotea sintenisii	4.5	0.458	N
	Coccoloba microstachya	3.4	0.667	N
GuaGui/DenArb	**Guarea guidonia**	46.3	0.001	N
	Dendropanax arboreus	18.7	0.017	N
	Inga vera	16.2	0.021	N
	Mangifera indica	12.4	0.056	I
	Urera baccifera	12.2	0.073	N
	Artocarpus altilis	7.6	0.248	I
	Erythrina poeppigiana	3.2	0.773	I
CecSch/CitSin	**Cecropia schreberiana**	45.7	0.001	N
	Citrus sinensis	28	0.004	I
	Inga laurina	11.9	0.057	N
	Cyathea arborea	9.9	0.121	N
	Persea americana	6.6	0.325	I
SyzJam	**Syzygium jambos**	71.4	0.001	I
	Zanthoxylum martinicense	7.9	0.172	N
	Schefflera morototonii	7.6	0.266	N
	Croton rigidus	5.7	0.375	N
	Calophyllum antillanum	4.5	0.556	I
PreMon/MicGar	**Prestoea montana**	71.5	0.002	N
	Micropholis garciniifolia	62.5	0.001	N
	Sloanea berteriana	61	0.001	N
	Micropholis chrysophylloides	46.4	0.001	N
	Henriettea squamulosum	43.6	0.001	N
	Byrsonima spicata	32.6	0.002	N
	Dacryodes excelsa	25.1	0.003	N
	Psychotria berteriana	22.5	0.01	N
	Alchornea latifolia	14.9	0.051	N
	Cordia borinquensis	12	0.076	N
	Clusia clusioides	8.4	0.216	N
	Myrcia citrifolia	4.3	0.536	N

Table 2
Tree species assemblages for mainland Puerto Rico, with importance value (IV), indicator species *P* (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Species	IV	P	Origin
Acacia farnesiana	87.5	0.001	I
Prosopis pallida	47.9	0.001	I
Albizia lebbeck	4.8	0.428	I
Leucaena leucocephala	76.7	0.001	N
Albizia procera	6.2	0.268	I
Citharexylum fruticosum	46.0	0.001	N
Exostema caribaeum	29.8	0.001	N
Ardisia obovata	16.9	0.007	N
Zanthoxylum martinicense	11.8	0.028	N
Pithecellobium dulce	7.4	0.178	I
Swietenia mahagoni	4.6	0.492	I
Bursera simaruba	37.6	0.001	N
Bucida buceras	25.9	0.001	N
Amyris elemifera	16.0	0.018	N
Coccoloba diversifolia	15.0	0.019	N
Ocotea sintenisii	9.4	0.054	N
Myrsine coriacea	8.3	0.122	N
Licaria parvifolia	8.2	0.098	N
Senna siamea	7.4	0.202	I
Pictetia aculeata	7.2	0.141	N
Ocotea coriacea	4.6	0.396	N
Thouinia striata	85.2	0.001	N
Ficus citrifolia	9.7	0.092	N
Petitia domingensis	7.0	0.185	N
Trichilia pallida	5.1	0.346	N
Eugenia rhombea	4.0	0.501	N
Coccoloba microstachya	3.4	0.605	N
Casearia guianensis	62.3	0.001	N
Andira inermis	16.9	0.018	N
Guazuma ulmifolia	15.9	0.018	N
Guapira fragrans	11.4	0.059	N
Myrcia splendens	9.4	0.096	N
Cupania americana	6.5	0.318	N

Assemblage	Species	IV	P	Origin
NeoRes/GueSca	**Neolaugeria resinosa**	52.5	0.001	N
	Guettarda scabra	42.3	0.001	N
	Eugenia monticola	37.8	0.001	N
	Tabebuia haemantha	25.5	0.001	N
	Pimenta racemosa	15.6	0.013	N
	Randia aculeata	13.8	0.022	N
	Clusia rosea	13.6	0.022	N
	Casearia decandra	7.8	0.120	N
	Bourreria succulenta	7.4	0.159	N
	Ocotea floribunda	6.6	0.237	N
	Annona muricata	3.7	0.607	N
	Homalium racemosum	3.7	0.567	N
SpaCam	**Spathodea campanulata**	76.6	0.001	I
	Terminalia catappa	4.6	0.381	I
TabHet/CasArb	**Tabebuia heterophylla**	62.9	0.001	N
	Casearia arborea	19.5	0.005	N
	Roystonea borinquena	6.0	0.301	N
	Myrcia citrifolia	5.2	0.333	N
CasSyl/PsiGua	**Casearia sylvestris**	20.5	0.004	N
	Psidium guajava	11.9	0.046	N
	Coffea arabica	11.6	0.039	I
	Ormosia krugii	8.5	0.161	N
	Eugenia biflora	7.2	0.212	N
	Thespesia grandiflora	4.6	0.448	n
	Buchenavia tetraphylla	3.6	0.583	N
	Hymenaea courbaril	3.6	0.672	N
	Tetrazygia elaeagnoides	2.3	0.907	N
	Piper amalago	1.9	0.953	N
GuaGui/DenArb	**Guarea guidonia**	49.0	0.001	N
	Dendropanax arboreus	21.0	0.003	N
	Mangifera indica	13.2	0.023	I
	Artocarpus altilis	10.1	0.082	I
	Cordia sulcata	6.4	0.368	N
	Quararibea turbinata	4.2	0.470	N
	Erythrina poeppigiana	3.0	0.786	I
	Cordia alliodora	2.1	0.913	N

Table 3
Tree species assemblages for the Virgin Islands, with importance value (IV), indicator species *P* (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Assemblage	Species	IV	P	Origin
ProPal	**Prosopis pallida**	86.6	0.001	I
AcaFar	**Acacia farnesiana**	81.2	0.001	I
	Albizia lebbeck	8.0	0.676	I
	Inga laurina	6.3	0.794	N
LeuLeu	**Leucaena leucocephala**	71.4	0.001	N
	Samanea saman	7.3	0.752	I
AcaMur/PisSub	**Acacia muricata**	84.5	0.001	N
	Pisonia subcordata	62.1	0.001	N
	Eugenia cordata	55.4	0.001	N
	Capparis cynophallophora	49.6	0.001	N
	Myrciaria floribunda	47.8	0.001	N
	Amyris elemifera	41.5	0.010	N
	Guettarda scabra	26.5	0.032	N
	Bucida buceras	15.3	0.322	N
CorAlb	**Cordia alba**	84.6	0.001	N
	Melicoccus bijugatus	25.2	0.089	I
	Croton astroites	16.4	0.154	N
	Eugenia rhombea	15.4	0.218	N
	Adelia ricinella	14.0	0.164	N
	Tecoma stans	8.8	0.597	N
EugMon/CapBad	**Eugenia monticola**	41.8	0.011	N
	Capparis baducca	35.3	0.014	N
	Bursera simaruba	32.1	0.018	N
	Maytenus laevigata	32.1	0.027	N
	Sabinea florida	29.4	0.019	N
	Ocotea coriacea	27.7	0.037	N
	Bourreria succulenta	26.0	0.069	N
	Chionanthus compactus	17.3	0.119	N
	Cordia alliodora	15.7	0.269	N
	Krugiodendron ferreum	14.5	0.213	N
GuaFra/CapInd	**Guapira fragrans**	64.7	0.001	N
	Capparis indica	34.7	0.039	N
	Cassine xylocarpa	19.0	0.128	N
	Tabebuia heterophylla	9.6	0.514	N
	Capparis hastata	9.3	0.466	N
CasGui/ZanMon	**Casearia guianensis**	48.0	0.001	N
	Zanthoxylum monophyllum	42.3	0.009	N
	Citharexylum fruticosum	40.0	0.009	N
	Ziziphus mauritiana	39.0	0.023	I
	Trichilia hirta	35.7	0.017	N
	Zanthoxylum martinicense	26.4	0.030	N
	Acacia macracantha	24.9	0.063	I
	Andira inermis	23.7	0.081	N
	Randia aculeata	12.4	0.336	N
	Swietenia mahagoni	10.6	0.385	I

Micropholis guyanensis (A. DC.) Pierre and *C. schreberiana* were positively correlated.

Ordination results of the plots on mainland Puerto Rico and all-islands data were similar (cumulative $R^2 = 0.435$). Axis 1 for this ordination was negatively correlated with spring minimum temperatures, similar but opposite in sign to the correlations found in all-islands axis 2 (Table 6). *G. guidonia* (positive correlation) and *L. leucocephala* (negative correlation) were associated with this axis. Puerto Rico axis 2 was positively correlated with distance from the coast, and negatively correlated with spring and annual moisture stress, and axis 3 was negatively correlated with winter and spring moisture stress, and it was positively correlated with latitude.

Ordination of the Virgin Islands plots showed environmental variable correlations with different axes from those of the all-islands axes or mainland Puerto Rico (Table 7). In addition, the correlations were stronger (cumulative $R^2 = 0.632$). Axis 1 was notably correlated with latitude, average monthly temperature in November, and slope. *L. leucocephala* was positively correlated with this axis, while a suite of dry forest species that included *B. simaruba*, *Guapira fragrans* (Dum.-Cours.) Little and *A. farnesiana* were negatively correlated with the axis. Axis 2 was correlated with precipitation in October and July, and latitude. *A. farnesiana* and *Acacia muricata* (L.) Willd. were positively correlated with this axis, and *L. leucocephala* was negatively correlated. Virgin Islands ordination axis 3 is significantly correlated with maximum spring and fall temperatures, and winter precipitation to a lesser extent.

3.3. Life zone, geology, forest age and land cover distribution

The frequency with which each species assemblages was found within the 8 life zone/geologic substrate combinations on Puerto Rico and the 4 life zone/geologic substrate combinations on the Virgin Islands is presented in Tables 8 and 9, respectively. The distribution of forested plots by the land cover type found before to reversion to forest shows the prevalence of abandoned pasture across mainland Puerto Rico (Table 10). All assemblages except the subtropical lower montane PreMon/MicGar were found on sites that had formerly been pasture or herbaceous agriculture. Some assemblages, notably GuaGui/DenArb, were frequently found in areas of abandoned coffee shade. Three assemblages (AcaFar/ProPal, LeuLeu and CecSch/CitSin) were not found in undisturbed (since 1951) forest.

There was strong indication that the AcaFar/ProPal assemblage of mainland Puerto Rico was found more frequently in the subtropical dry forest life zone ($P = 0.0588$), and that it had little preference as to geologic substrate ($P = 0.8669$). In all cases, the AcaFar/ProPal assemblage was found on land that had reverted from agriculture or pasture. Similarly, there was a strong indication that the AcaFar assemblage found on the Virgin Islands was preferentially distributed in subtropical dry forest ($P = 0.0588$), and showed no differences in distribution by substrate. The ProPal assemblage of the Virgin Islands was found entirely within the subtropical dry forest life zone on all substrates.

The Puerto Rico LeuLeu assemblage was distributed in both the subtropical dry and moist forest life zones on a variety of substrates, entirely on land that was formerly herbaceous agricultural/pasture. The LeuLeu assemblage was distributed similarly in the Virgin Islands, however, with a markedly higher frequency on extrusive volcanic substrates than on limestone, intrusive volcanic or alluvial substrates ($P = 0.0003$).

Some of the Virgin Islands assemblages were found with equal frequency in the subtropical dry and moist forest life zone (AcaMur/PisSub, EugMon/CapBad, and CasGui/ZanMon), and two other assemblages (CorAlb and GuaFra/CapInd) might also straddle these life zones but there were too few occurrences for statistical testing. There were significant differences in the distribution by substrate of these Virgin Island assemblages. The AcaMur/PisSub assemblage occurred exclusively on extrusive volcanic substrates. The EugMon/CapBad assemblage was more common on extrusive volcanic substrates ($P = 0.0076$), while the CasGui/ZanMon assemblage showed greater frequency of occurrence on intrusive volcanic substrates ($P = 0.0464$).

Puerto Rico mainland assemblages that straddled the subtropical dry and moist forest life zones were CitFru/ExoCar, BurSim/BucBuc, and ThoStr. Additionally, there was some indication that the CitFru/ExoCar assemblage was more frequently found on former herbaceous agricultural/pasture land ($P = 0.0578$), but it was also found in areas that had been forest since 1951. This assemblage showed little preference for substrate type within the subtropical dry and moist forest life zones. The BurSim/BucBuc assemblage was found on both limestone and extrusive volcanic substrates, but had a markedly higher occurrence on limestone in the subtropical moist forest life zone ($P = 0.0186$). This assemblage

Table 4
Number of plots sampled, quadratic mean diameter (QMD, cm), and mean values for trees per hectare (TPH), basal area per hectare (BA, m^2/ha), aboveground live biomass per hectare (AGBH, Mg/ha), canopy height (HT, m), and annual moisture stress index (MS), with standard errors of the mean for groups on all islands, mainland Puerto Rico and the Virgin Islands.

Island group	N	QMD	TPH	BAH	AGBH	HT	MS
All islands							
ProPal	7	5.3	2231 (705)	5.0 (2.0)	25.2 (10.8)	4.4 (0.5)	0.0267 (0.0016)
AcaFar	15	5.4	2471 (554)	5.6 (1.1)	22.9 (4.9)	5.0 (0.5)	0.0253 (0.0013)
CorAlb/MelBij	4	4.9	4862 (1379)	9.3 (3.7)	33.1 (13.0)	4.4 (0.3)	0.0246 (0.0005)
AcaMur/PisSub	7	6.5	6191 (344)	20.4 (2.1)	75.9 (9.6)	6.3 (0.5)	0.0230 (0.0007)
LeuLeu	41	4.8	4235 (478)	7.6 (0.8)	31.3 (3.4)	5.3 (0.2)	0.0228 (0.0005)
BucBuc	15	5.9	4102 (740)	11.1 (2.2)	47.7 (10.2)	6.4 (0.7)	0.0226 (0.0010)
GuaFra/MayLae	12	8.4	3741 (547)	21.0 (3.0)	80.9 (10.7)	8.2 (0.8)	0.0221 (0.0008)
CitFru/SwiMah	7	10.3	1608 (620)	13.5 (4.0)	44.0 (12.8)	8.8 (0.8)	0.0197 (0.0007)
ZanMon	31	7.1	4190 (433)	16.7 (1.7)	71.4 (8.8)	8.7 (0.6)	0.0187 (0.0009)
EugMon/BouSuc	15	6.0	4891 (729)	14.0 (2.1)	53.1 (7.8)	7.5 (0.5)	0.0179 (0.0011)
CasGui/TriHir	15	7.4	4228 (627)	18.1 (3.3)	74.3 (15.2)	10.2 (0.6)	0.0163 (0.0015)
TabHet	8	7.8	2510 (1031)	11.9 (2.7)	48.6 (12.5)	9.7 (1.4)	0.0145 (0.0030)
TabHae/PimRac	9	6.9	4677 (674)	17.4 (3.1)	77.6 (15.4)	9.0 (1.3)	0.0144 (0.0009)
SpaCam	27	10.8	3740 (533)	34.3 (3.4)	151.7 (17.4)	13.4 (1.0)	0.0137 (0.0004)
ThoStr/CasSyl	23	9.6	3461 (351)	25.0 (7.7)	86.1 (17.7)	10.7 (0.6)	0.0132 (0.0005)
CasArb	25	10.4	2755 (417)	23.3 (3.2)	94.9 (12.7)	11.1 (0.8)	0.0128 (0.0009)
MicPra	24	8.8	2961 (354)	18.1 (2.0)	77.7 (8.8)	11.9 (0.8)	0.0126 (0.0003)
GuaGui/DenArb	41	10.9	3078 (335)	28.8 (2.9)	114.1 (11.0)	13.0 (0.5)	0.0125 (0.0002)
CofAra/RoyBor	4	10.1	1299 (437)	10.3 (4.4)	33.6 (12.2)	11.3 (1.5)	0.0124 (0.0011)
SyzJam	10	12.2	2541 (463)	29.7 (6.8)	123.3 (27.8)	13.6 (1.4)	0.0122 (0.0005)
CecSch/CitSin	11	11.3	1579 (452)	15.9 (3.5)	70.3 (18.0)	11.6 (1.4)	0.0120 (0.0006)
PreMon/MicGar	8	11.6	2519 (389)	26.6 (3.7)	111.7 (17.2)	10.8 (0.8)	0.0070 (0.0009)
Puerto Rico							
AcaFar/ProPal	8	6.4	1977 (436)	6.4 (1.8)	27.6 (8.2)	5.7 (0.9)	0.0252 (0.0028)
LeuLeu	19	5.4	3359 (755)	7.7 (1.9)	34.3 (8.9)	6.2 (0.6)	0.0205 (0.0012)
CitFru/ExoCar	14	7.0	3587 (649)	13.9 (2.3)	57.1 (10.1)	8.9 (0.9)	0.0190 (0.0013)
BurSim/BucBuc	20	7.1	4389 (558)	17.3 (1.9)	77.4 (9.0)	9.3 (0.7)	0.0184 (0.0010)
ThoStr	7	7.3	3808 (900)	15.9 (1.9)	64.7 (9.1)	8.7 (0.8)	0.0158 (0.0022)
CasGui/AndIne	13	7.5	4331 (720)	19.2 (3.8)	79.3 (17.2)	10.7 (0.6)	0.0155 (0.0016)
NeoRes/GueSca	17	6.6	4025 (626)	13.7 (2.2)	58.5 (10.2)	8.6 (0.8)	0.0138 (0.0006)
SpaCam	43	10.2	3635 (372)	29.6 (2.5)	130.0 (12.3)	12.8 (0.7)	0.0133 (0.0003)
TabHet/CasArb	12	8.7	3060 (747)	18.0 (3.7)	69.8 (15.2)	10.0 (0.9)	0.0130 (0.0020)
CasSyl/PsiGua	29	10.1	3002 (407)	24.1 (6.2)	84.0 (15.4)	10.8 (0.7)	0.0129 (0.0006)
GuaGui/DenArb	46	11.1	3066 (316)	29.6 (2.7)	117.8 (10.3)	13.4 (0.5)	0.0126 (0.0002)
SyzJam	19	11.0	2425 (315)	23.2 (4.4)	97.9 (19.3)	12.6 (0.9)	0.0120 (0.0004)
CecSch/CitSin	14	11.0	1476 (365)	14.0 (2.9)	62.7 (14.7)	11.8 (1.1)	0.0119 (0.0005)
PreMon/MicGar	9	11.1	2570 (347)	25.0 (3.7)	103.6 (17.2)	10.4 (0.8)	0.0073 (0.0009)
Virgin Islands							
GuaFra/CapInd	5	7.7	2349 (225)	10.9 (4.2)	38.2 (13.3)	5.4 (0.7)	0.0262 (0.0013)
ProPal	6	5.4	2479 (780)	5.7 (2.2)	29.0 (11.9)	4.6 (0.5)	0.0254 (0.0012)
CorAlb	4	4.9	4862 (1379)	9.3 (3.7)	33.1 (13)	4.4 (0.3)	0.0246 (0.0005)
AcaFar	7	4.0	2768 (1137)	3.5 (1.2)	11.9 (4.3)	3.7 (0.5)	0.0243 (0.0007)
LeuLeu	29	4.9	4670 (521)	8.7 (0.9)	35.2 (3.9)	5.3 (0.2)	0.0236 (0.0003)
AcaMur/PisSub	7	6.5	6191 (343)	20.4 (2.1)	75.9 (9.6)	6.3 (0.5)	0.0230 (0.0007)
CasGui/ZanMon	14	7.6	2465 (250)	11.1 (1.8)	40.0 (5.6)	6.4 (0.4)	0.0229 (0.0007)
EugMon/CapBad	17	7.0	5397 (535)	20.7 (2.1)	79.9 (7.2)	7.5 (0.3)	0.0222 (0.0004)

most frequently originated on land that had formerly been in herbaceous agriculture or pasture, followed by land that had remained forested since 1951 ($P = 0.0078$). The ThoStr assemblage had broad distributions across the subtropical dry, moist and wet/rain forest life zones, and was found on both volcanic and limestone substrates, and all past land uses, with no significant differences.

Other mainland Puerto Rico assemblages showed more general distributions across the broad subtropical moist forest life zone. The CasiGui/AndIne assemblage occupied abandoned herbaceous agricultural/pasture land ($P = 0.0012$) in the subtropical moist forest life zone ($P = 0.0388$) with equal frequency on volcanic, alluvial and limestone substrates ($P = 0.7212$). The NeoRes/GueSca assemblage was found primarily in the subtropical moist forest life zone ($P = 0.0221$) on former herbaceous agricultural/pasture land, land that has been forested since 1951, and to a lesser extent, abandoned coffee shade ($P = 0.0468$). While there is some indication that this assemblage primarily forms on limestone and ultramafic substrates ($P = 0.0897$), it was found on alluvial and volcanic substrates as well. The TabHet/CasArb assemblage had broad distributions across the subtropical dry, moist and wet/rain forest life zones, was found on both volcanic and limestone substrates, and all past land uses, with no significant differences. Although the CasSyl/PsiGua assemblage was frequently found on abandoned pasture, it was not exclusive to the former land use, being found on abandoned coffee shade and relatively undisturbed forest ($P = 0.1690$). It did, however, show greater frequency of occurrence in the moist forest life zone on extrusive volcanic, followed by limestone, substrates ($P < 0.0001$).

The plots with high relative importance of the introduced species *S. campanulata*, the SpaCam assemblage, occurred most frequently in the subtropical moist forest life zone on both limestone and extrusive volcanic substrates, with a very strong affinity for former herbaceous agricultural/pasture land ($P = 0.0006$). This assemblage was also found, although much less frequently, in subtropical wet forest on extrusive volcanic substrates in abandoned coffee shade.

A number of assemblages were encountered on lands formerly managed for shade coffee production, particularly the GuaGui/DenArb assemblage. This assemblage was found in the subtropical

Table 5
Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for all islands.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Moisture stress—Spring	−0.550	0.303	Temperature, min.—March	0.440	0.193	Temperature, max.—September	−0.277	0.077
Moisture stress—Annual	−0.539	0.291	Temperature, min.—January	0.436	0.190	Temperature, max.—June	−0.277	0.077
Moisture stress—Summer	−0.463	0.215	Temperature, min.—November	0.435	0.189	Elevation	0.272	0.074
Moisture stress—Winter	−0.464	0.215	Temperature, min.—Annual	0.432	0.187	Temperature, max.—May	−0.271	0.074
Moisture stress—Fall	−0.444	0.197	Temperature, min.—December	0.432	0.187	Temperature, max.—October	−0.273	0.074
Precipitation—April	0.411	0.169	Temperature, min.—February	0.432	0.186	Temperature, max.—April	−0.270	0.073
Coast distance	0.398	0.158	Temperature, min.—September	0.431	0.186	Temperature, max.—August	−0.268	0.072
Precipitation—May	0.393	0.154	Temperature, min.—April	0.430	0.185	Temperature, avg.—June	−0.265	0.070
Temperature, min.—June	−0.384	0.147	Temperature, min.—October	0.426	0.181	Temperature, avg.—May	−0.264	0.070
Temperature, min.—October	−0.371	0.138	Temperature, min.—August	0.420	0.176	Temperature, max.—July	−0.264	0.070
Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Leucaena leucocephala	−0.501	0.251	*Guarea guidonia*	−0.366	0.134	*Spathodea campanulata*	−0.594	0.353
Guarea guidonia	0.449	0.202	*Bursera simaruba*	0.325	0.106	*Leucaena leucocephala*	−0.250	0.062
Casearia guianensis	0.325	0.106	*Cecropia schreberiana*	−0.322	0.103	*Inga laurina*	−0.234	0.055
Acacia farnesiana	−0.287	0.082	*Ing a vera*	−0.319	0.101	*Micropholis guyanensis*	0.224	0.050
Andira inermis	0.281	0.079	*Tabebuia heterophylla*	0.308	0.095	*Cecropia schreberiana*	0.223	0.050
Dendro panax arboreus	0.251	0.063	*Guettarda scabra*	0.307	0.094	*Ocotea leucoxylon*	0.218	0.047
Mangifera indica	0.225	0.051	*Spathodea campanulata*	−0.279	0.078	*Prestoea montana*	0.211	0.045
Prosopis pallida	−0.219	0.048	*Coccolo ba diversifolia*	0.269	0.072	*Inga laurina*	0.211	0.044
Bursera simaruba	−0.216	0.047	*Ardisia obovata*	0.265	0.070	*Tabebuia heterophylla*	−0.209	0.044
Bucida buceras	−0.216	0.047	*Citrus sinen sis*	−0.246	0.060	*Albizia procera*	−0.205	0.042
	Axis r^2 = 0.198			Axis r^2 = 0.146			Axis r^2 = 0.09	

moist and wet/rain forest life zones on all substrates except for ultramafic. This assemblage showed markedly high frequency of occurrence in the subtropical moist forest life zone on extrusive volcanic soils on former herbaceous agricultural/pasture land, followed closely by a strong presence in the subtropical wet/rain forest life zone, on extrusive volcanic substrates in abandoned coffee shade ($P = 0.0011$). Another assemblage found in the former coffee producing lands was the CecSch/CitSin. This assemblage was found most frequently in abandoned coffee shade on volcanic substrates in the subtropical wet/rain life zone, and less frequently on former herbaceous agricultural/pasture land on limestone substrates ($P = 0.0159$) in the subtropical moist life zone.

The assemblage SyzJam, with its high relative importance of the introduced *S. jambos*, was also found most frequently on former agricultural/pasture land, with fewer occurrences in abandoned coffee shade, and two instances in land that had been forest since

Table 6
Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for mainland Puerto Rico.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Temperature, min.—April	−0.547	0.300	Coast distance	0.389	0.152	Moisture stress—Winter	−0.259	0.067
Temperature, min.—May	−0.547	0.300	Moisture stress—Spring	−0.363	0.132	Moisture stress—Spring	−0.233	0.055
Temperature, min.—March	−0.544	0.296	Moisture stress—Annual	−0.347	0.120	Latitude	0.229	0.052
Temperature, min.—Annual	−0.543	0.295	Moisture stress—Winter	−0.316	0.100	Moisture stress—Annual	−0.199	0.040
Temperature, min.—October	−0.543	0.295	Moisture stress—Summer	−0.282	0.080	Slope	0.197	0.039
Temperature, min.—February	−0.536	0.288	Precipitation—April	0.277	0.077	Slope position	0.182	0.033
Temperature, min.—June	−0.537	0.288	Moisture stress—Fall	−0.278	0.077	Moisture stress—Summer	−0.164	0.027
Temperature, min.—September	−0.536	0.287	Latitude	0.246	0.061	Slope percent	0.162	0.026
Temperature, min.—November	−0.531	0.282	Precipitation—May	0.235	0.055	Precipitation—April	0.133	0.018
Temperature, min.—August	−0.530	0.281	Temperature, min.—October	−0.220	0.049	Precipitation—December	0.130	0.017
Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Guarea guidonia	0.445	0.198	*Spathodea campanulata*	0.601	0.361	*Casearia guianensis*	0.393	0.154
Leucaena leucocephala	−0.425	0.181	*Guarea guidonia*	0.373	0.139	*Leucaena leucocephala*	−0.360	0.130
Cecropia schreberiana	0.341	0.116	*Bucida buceras*	−0.289	0.084	*Andirainermis*	0.333	0.111
Eugenia jambos	0.307	0.094	*Bursera simaruba*	−0.277	0.076	*Acacia farnesiana*	−0.293	0.086
Ingavera	0.305	0.093	*Exostema caribaeum*	−0.240	0.057	*Tabebuia heterophylla*	0.264	0.070
Ingalaurina	0.302	0.091	*Clusiarosea*	−0.235	0.055	*Myrcia splendens*	0.255	0.065
Ocotea leucoxylon	0.293	0.086	*Eugenia monticola*	−0.233	0.054	*Citharexylum fruticosum*	0.232	0.054
Tabebuia heterophylla	−0.270	0.073	*Casearia sylvestris*	0.211	0.044	*Spathodea campanulata*	−0.220	0.049
Bursera simaruba	−0.264	0.070	*Guettarda scabra*	−0.210	0.044	*Citrussinensis*	−0.205	0.042
Dendropanax arboreus	0.240	0.057	*Pictetia aculeata*	−0.202	0.041	*Ardisiaobovata*	0.200	0.040
	Axis r^2 = 0.163			Axis r^2 = 0.144			Axis r^2 = 0.128	

Table 7

Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for the Virgin Islands.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Latitude	−0.558	0.311	Precipitation–October	−0.318	0.101	Temperature, max.–May	−0.623	0.389
Temperature, avg.–November	0.504	0.254	Latitude	0.272	0.074	Temperature, max.–November	−0.621	0.385
Slope	−0.503	0.253	Precipitation–July	−0.243	0.059	Precipitation–February	0.619	0.383
Elevation	−0.478	0.228	Moisture stress–summer	0.216	0.047	Temperature, max.–March	−0.600	0.360
Moisture stress–Spring	0.474	0.225	Moisture stress–Fall	0.210	0.044	Temperature, max.–April	−0.591	0.350
Slope percent	−0.472	0.222	Precipitation–June	−0.207	0.043	Longitude	0.589	0.347
Temperature, avg.–May	0.431	0.186	Slope position	−0.207	0.043	Temperature, max.–October	−0.573	0.328
Temperature, avg.–December	0.414	0.172	Precipitation–September	−0.197	0.039	Temperature, max.–June	−0.563	0.317
Precipitation–April	−0.394	0.155	Temperature, max.–August	0.184	0.034	Precipitation–November	0.562	0.316
Temperature, avg.–March	0.392	0.154	Distance from coast	−0.181	0.033	Temperature, max.–Annual	−0.564	0.310

Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Leucaena leucocephala	0.597	0.357	*Leucaena leucocephala*	−0.630	0.397	*Prosopis pallida*	−0.675	0.455
Bursera simaruba	−0.496	0.246	*Acacia farnesiana*	0.542	0.293	*Bourreria succulenta*	0.417	0.174
Guapira fragrans	−0.487	0.237	*Acacia muricata*	0.320	0.103	*Ziziphus mauritiana*	−0.350	0.122
Acacia farnesiana	0.363	0.132	*Cassine xylocarpa*	0.288	0.083	*Trichilia hirta*	−0.273	0.074
Myrciaria floribunda	−0.327	0.107	*Prosopis pallida*	0.249	0.062	*Guettarda scabra*	0.267	0.071
Maytenus laevigata	−0.319	0.102	*Melicoccus bijugatus*	−0.233	0.054	*Eugenia monticola*	0.260	0.068
Capparis baducca	−0.319	0.101	*Amyris elemifera*	0.232	0.054	*Pisonia subcordata*	0.253	0.064
Capparis cynophallophora	−0.289	0.083	*Guapira fragrans*	0.222	0.049	*Krugiodendron ferreum*	0.245	0.060
Cordia alliodora	−0.279	0.078	*Guettarda scabra*	0.212	0.045	*Acacia farnesiana*	−0.235	0.055
Acacia muricata	−0.276	0.076	*Eugenia cordata*	0.213	0.045	*Casearia guianensis*	−0.235	0.055
	Axis r^2 = 0.269			Axis r^2 = 0.189			Axis r^2 = 0.174	

Table 8

Frequency distribution of species assemblages by Holdridge life zone and geology on mainland Puerto Rico.

Assemblage	Life zone/geologic substrate								
	Dry/AVS	Dry/Lime	Dry, Moist/Ultra	Moist/AVS	Moist, Wet/Lime	Wet/AVS	LM/AVS	Wet, LM/Ultra	Totals
AcaFar/ProPal	4	2	0	2	0	0	0	0	8
LeuLeu	5	4	3	7	0	0	0	0	19
CitFru/ExoCar	0	2	2	4	6	0	0	0	14
BurSim/BucBuc	4	3	0	2	11	0	0	0	20
ThoStr	0	1	0	3	3	0	0	0	7
CasGui/AndIne	1	0	0	4	5	3	0	0	13
NeoRes/GueSca	1	0	3	2	7	0	0	4	17
SpaCam	0	0	0	17	14	12	0	0	43
TabHet/CasArb	0	1	0	5	1	5	0	0	12
CasSyl/PsiGua	0	1	0	12	8	7	0	1	29
GuaGui/DenArb	0	0	0	20	7	19	0	0	46
SyzJam	0	0	0	3	7	9	0	0	19
CecSch/CitSin	0	0	0	0	3	9	2	0	14
PreMon/MicGar	0	0	0	0	0	4	4	1	9
Totals	15	14	8	81	72	68	6	6	270

These groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical dry–moist on ultramafic (Dry, Moist/Ultra), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moistwet on limestone (Moist, Wet/Lime), subtropical wet on alluvial, volcanic and sedimentary (Wet/AVS), lower montane on alluvial, volcanic and sedimentary (LM/AVS), and subtropical wet–lower montane on ultramafic (Wet, LM/Ultra).

1951. It occurred with equal frequency in the subtropical moist and wet/rain life zones ($P = 0.6374$), but most frequently on extrusive volcanic substrates ($P = 0.0155$). Finally, the assemblage distributed at the highest elevation and highest precipitation, the PreMon/MicGar, was found in the subtropical wet/rain and subtropical lower montane life zones with equal frequency, entirely on volcanic substrates. All of the sites with this assemblage had been forested since 1951.

4. Discussion

The new forest tree species assemblages that formed on Puerto Rico and the U.S. Virgin Islands show broadly defined, general species assemblages that span multiple islands, with unique variations created by local environmental factors and differing land-use histories.

4.1. Highly disturbed subtropical dry forest assemblages

Assemblages characterized by the importance of *A. farnesiana*, *P. pallida* and *L. leucocephala* were found on all islands on relatively flat, lowland sites with greater spring moisture stress, grazing and herbaceous agriculture land-use histories and, in some cases, succession arrested by chronic disturbance. These are resilient, successional species capable of persisting and competing successfully with other taxa in pastures and disturbed sites along the islands' coastlines and dry limestone areas (Dansereau, 1966; Skolmen, 1990; Parrotta, 2000a,b). Dense stands of *L. leucocephala* forming on drier, highly disturbed lands have been described on Puerto Rico (Molina and Lugo, 2006) and the U.S. Virgin Islands (Ray and Brown, 1995; Adam and Ryan, 2003; Thomas and Devine, 2005; Weaver, 2006a). The *A. farnesiana* and *P. pallida* stands had relatively low TPH and BAH (2231–2471 stems/ha and

Table 9
Frequency distribution of species assemblages by Holdridge life zone and geology in the Virgin Islands.

Assemblage	Life zone/geologic substrate				
	Dry/ AVS	Dry/ Lime	Moist/ AVS	Moist, Wet/Lime	Totals
GuaFra/CapInd	4	0	1	0	5
ProPal	6	0	0	0	6
CorAlb	3	1	0	0	4
AcaFar	4	2	1	0	7
LeuLeu	12	8	8	1	29
AcaMur/PisSub	4	0	3	0	7
CasGui/ZanMon	8	0	6	0	14
EugMon/CapBad	7	0	10	0	17
Totals	48	11	29	1	89

Life zone/geologic substrate groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moist–wet on limestone (Moist, Wet/Lime).

Table 10
Frequency distribution of forested inventory plots by last land cover class before reverting to forest, by assemblage, on mainland Puerto Rico.

Assemblage	HerbAg/ pasture	Coffee shade	Not disturbed	Other	Total
AcaFar/ProPal	7	0	0	1	8
LeuLeu	15	0	0	4	19
CitFru/ExoCar	8	0	3	3	14
BurSim/BucBuc	13	2	5	0	20
ThoStr	4	1	1	1	7
CasGui/AndIne	10	1	1	1	13
NeoRes/GueSca	9	1	6	1	17
SpaCam	27	8	1	7	43
TabHet/CasArb	5	5	1	1	12
CasSyl/PsiGua	13	5	9	2	29
GuaGui/DenArb	22	16	6	2	46
SyzJam	11	5	2	1	19
CecSch/CitSin	4	9	0	1	14
PreMon/MicGar	0	0	8	1	9
Totals	148	53	43	26	270

5.0–5.6 m^2/ha, across all islands). *L. leucocephala*, while forming denser stands (4235.1 stems/ha), had the lowest QMD (4.8 cm) and low BAH (7.6 m^2/ha).

There are surprisingly few assemblages found entirely within the subtropical dry forest life zone on mainland Puerto Rico beyond the highly impacted forests dominated by introduced species previously mentioned. Instead, Puerto Rico's subtropical dry forest life zone held assemblages that were also found in the subtropical moist forest life zone, or more correctly stated, across the broad transition zone between subtropical dry and subtropical moist forest.

4.2. Subtropical dry and dry–moist transition forest assemblages

Within the broad transition zone between the subtropical dry and subtropical moist forest life zones in Puerto Rico, and to a lesser extent the Virgin Islands, there has been the formation of more diverse assemblages of Caribbean dry forest species on lower slopes less impacted by human land use and disturbance and less dominance by introduced pioneer species. There is indication of some species composition continuity across the subtropical dry and moist forests on all the islands. Broad assemblages defined by the relatively higher importance of *C. guianensis*, *Eugenia monticola* (Sw.) DC. and *G. fragrans* were found on all islands. The *Bucida buceras*–*G. fragrans* community described by Gould et al. (2006) has species from both the Puerto Rico mainland and Virgin islands subtropical dry to moist forest assemblages found in this study.

Natives *B. buceras* L. and *B. simaruba* are often dominant trees in Caribbean subtropical dry to moist forests (Francis, 2000a,b; Gould et al., 2006), and these species figure prominently in some of the assemblages found in this study. On mainland Puerto Rico, the distribution of the BurSim/BucBuc assemblage reflects interplay between climate and substrate. The assemblage was found in both life zones, but in the subtropical moist forest it was more frequently found on droughty limestone substrates. This assemblage was more common on limestone substrates and on sites in the oldest forest class.

The Virgin Islands showed some unique subtropical dry–moist transitional forest assemblages that had a markedly different species composition than those on mainland Puerto Rico, for example, AcaMur/PisSub, EugMon/CapBad, CorAlb and GuaFra/CapInd. This may be due to differing patterns of land use, rates of forest recovery, and geographic isolation of each island. The Virgin Islands subtropical dry to moist assemblages found here were similar to those found by Weaver (2006b) in the Cinnamon Bay watershed, St. John. But, we did not observe the same patterns of species distribution by topography seen by Weaver and Chinea (1987) and Weaver (2006b), assemblage differentiation into the toposequences described by Ray and Brown (1995), or the correlations between assemblages and substrates found by Woodbury and Weaver (1987).

Although we did not have the detailed land-use history for these islands that we had for mainland Puerto Rico, we do know from historical sources that agriculture abandonment began sooner and proceeded quicker on St. John than on the other Virgin Islands, meaning the secondary forests have been recovering there for a longer time (Weaver, 2006b). This decreased level of recent disturbance, particularly within the protected Virgin Islands National Park, presents a skewed, but species-rich, example of Virgin Islands subtropical dry and subtropical moist forest under reduced human impacts and after greater recovery times.

4.3. Subtropical moist forest assemblages

The assemblages in the extensive subtropical moist forest life zone on Puerto Rico often occupied a variety of substrates and were found across multiple life zones. The ThoStr, CasGui/AndIne, TabHet/CasArb and CasSyl/PsiGua assemblages, while predominately found in the subtropical moist forest life zone, are also found to a lesser degree in the adjacent subtropical dry and subtropical wet life zones. The NeoRes/GueSca assemblage represents the vegetation on a combination of karst and ultramafic substrates in the subtropical moist to wet life zone of mainland Puerto Rico. This assemblage has species typically found on the droughty substrates of karst "mogote" hilltops and sides (Chinea, 1980; Álvarez Ruiz et al., 1997; Brandeis, 2006; Aukema et al., 2007).

Many subtropical moist and some wet forest sites on mainland Puerto Rico shared a relatively high importance of *S. campanulata*, particularly in the subtropical moist forest life zone on both limestone and extrusive volcanic substrates in former agricultural and pasture land, and in the subtropical wet forest on extrusive volcanic soil in abandoned coffee shade. The increase in importance of *S. campanulata* throughout the subtropical moist and wet forest life zones on mainland Puerto Rico has been observed since forest inventories began in 1980, and the species has held the position of most prevalent forest tree since the 1990 forest inventory (Birdsey and Weaver, 1982; Franco et al., 1997; Brandeis et al., 2007). *S. campanulata* grows best on deep, fertile, well-drained substrates, can colonize highly eroded sites, and commonly colonizes abandoned pastures (Dansereau, 1966; Francis, 2000c; Abelleira Martínez and Lugo, 2008). The *S.*

campanulata stands inventoried by this study were particularly productive, having the highest average AGBH (130 Mg/ha) and one of the highest BAH (29.6 m^2/ha). This is impressive considering that 81.4% of these stands were agricultural land in 1951, and 25.6% were still under agriculture as late as 1977. Abelleira Martínez and Lugo (2008) observed even higher productivity in *S. campanulata* stands growing on land formerly cultivated for sugar cane that averaged 91.9 m^2/ha of basal area.

Growth and regeneration of *S. campanulata* is limited, however, by shade intolerance that restricts its ability to replace itself in a mature stand (Francis, 2000c), even those periodically disturbed by hurricanes (Thompson et al., 2007). Brandeis (2006) observed that in the northwestern karst region *S. campanulata* was the most important tree species on the valley areas between mogote hills, but not on moderate, moister slopes where GuaGui/DenArb assemblage predominates, or on the drier, strongly sloped hilltops occupied by assemblages indicated by the relative importance of *T. heterophylla*. Despite their ability to persist in the understory for many years, *S. campanulata* seedlings and saplings are kept from regenerating by residual coffee shade canopies and replaced over time by more shade tolerant species, particularly *G. guidonia* (Rivera and Aide, 1998; Aide et al., 2000; Francis, 2000c; Marcano Vega et al., 2002), and *T. heterophylla* tolerates poorer soils (Weaver, 2000b) than *S. campanulata*.

4.4. Subtropical wet forest assemblages

This life zone holds young secondary forests where some overstory canopy has been maintained but that is now reverting to a more closed canopy condition with native species, and similar forests that have had their canopies more severely disturbed and opened to early successional native species. It also has forests that are typified by a naturalized shade tolerant species that is replacing itself well and becoming dominant in stands.

The GuaGui/DenArb assemblage is found on moderate, wetter mountain slopes and often indicates sites that were managed for coffee shade but that have now been largely abandoned. The maintenance of a tree overstory for coffee shade and high site productivity explain why this assemblage has the greatest HT (13.6 m), as well as high QMD (11.1 cm), BAH (29.6 m^2/ha), and AGBH (118 Mg/ha). These forests frequently grow on fertile volcanic substrates, experience low levels of moisture stress, and have been managed to maintain a tree overstory. Half of plots measured were still coffee shade or forest in 1951, and 84.8% were still coffee shade in 1977. By 1991, however, none of the plot locations were still being managed for coffee shade and all sites had reverted to unmanaged forest.

The importance of *G. guidonia* is a possible indication of how much the forests of Puerto Rico have been modified by former land uses, in this case coffee cultivation. Normally, *G. guidonia* is an uncommon component in undisturbed humid lowland and subtropical lower montane forests throughout its extensive natural range (Weaver, 2000a). In Puerto Rico, the species is found in association with *Dacryodes excelsa* Vahl and the other species typical of the "tabonuco" forest type and regeneration appears to be related to disturbance (Weaver, 2000a). *G. guidonia*, a native species that was maintained for coffee shade along with native *Inga laurina* (Sw.) Willd., and the introduced *Inga vera* Willd. and *Erythrina poeppigiana* (Walp.) O.F. Cook, has increased in importance to become the second most important species island-wide, indicating an ability to successfully regenerate in abandoned coffee shade and out-compete those other species (Birdsey and Weaver, 1982; Franco et al., 1997; Pascarella et al., 2000; Brandeis et al., 2007). This native species has responded to the regeneration opportunities provided by human forest management and disturbance that might have otherwise been taken by introduced species.

The CecSch/CitSin assemblage is an even more disturbed forest community within the former coffee shade areas. *C. schreberiana* is an early invader of disturbed areas and is often associated with other secondary forest species like *Schefflera morototonii* (Aubl.) Maguire, Steyermark & Frodin and *Ochroma pyramidale* (Cav. ex Lam.) Urban (Crowe, 1980; Liegel, 2000; Silander and Lugo, 2000). The presence of species that require light in the understory for germination and early growth like *C. schreberiana* indicate frequent canopy openings due to human activities or hurricanes (Crowe, 1980; Dallmeier et al., 1998; Weaver, 1998). This assemblage has a low TPH (1476 stems/ha) and low BAH (14.0 m^2/ha) relative to other assemblages in this life zone, but still a relatively high QMD (11.0 cm) and HT (11.8 m). These structural characteristics also point to a forest with more open canopy comprised of fewer, large trees that have been purposely retained or that have survived disturbances. Popper et al. (1999) found large, old, *C. schreberiana*, *S. morototonii* and *I. laurina* trees in association with coffee shade, and postulated that these trees were remnants of the prior, undisturbed forest, or that they had become established soon after abandonment.

An assemblage indicative of human impact and introduced species naturalization is characterized by the importance of the introduced species *Syzygium jambos* (L.) Alston. This shade tolerant species is capable of reproducing under closed canopies and of self-replacement to form dense, monospecific stands (Wadsworth, 1943; Aide et al., 2000; Pascarella et al., 2000; Brown et al., 2006; Thompson et al., 2007). We can see how the *S. jambos*-dominated assemblage is present not only on lands that were in agriculture in 1951 and 1977, but also on lands that had been coffee shade. This species has formed well-developed stands on fertile volcanic substrates. *S. jambos* has grown in importance since being described as a potentially important timber species by Wadsworth (1943) and currently ranks as the 8th most important species island-wide in the subtropical moist forest life zone and the 4th most important species in the subtropical wet forest life zone (Brandeis et al., 2007).

4.5. Subtropical lower montane forest assemblages

At higher elevations above the region of coffee cultivation, anthropogenic disturbances were limited to pasturing and wood cutting, so modifications to the forest were less notable. The sites with the PreMon/MicGar assemblage were all forested in 1951 and have remained so until today. The extensive, objective sampling of the entire landscape used in this study was not intensive enough within the upper elevation forests (even after some sampling intensification), to separate the traditionally described forest types of "tabonuco", "palo colorado", palm brake and elfin forests (Ewel and Whitmore, 1973; Weaver and Murphy, 1990; Weaver, 1991), or into the groups defined by the finer scale recent study by Gould et al. (2006). Instead, species indicative of all of these forest types such as *Prestoea montana* (Graham) Nichols., *Micropholis garciniifolia* Pierre, *Sloanea berteriana* Choisy ex DC., *D. excelsa* and many others were clustered together in one large, assemblage.

4.6. Environmental correlations to the species assemblages

Forest ecosystems on Puerto Rico and the U.S. Virgin Islands consist of broad tree species assemblages that can be found across all islands, and variations that have been created by differing land uses and individual island environmental conditions. Spring moisture stress was a prominent factor in the formation of assemblages, but so were maximum and minimum temperatures, and the topographic variables such as elevation and distance from the coast that are confounded with them. Highly disturbed, dry, relatively flat, lowland sites with greater spring moisture stress with assemblages indicated by *A. farnesiana*, *P. pallida* and *L. leucocephala* occupy one end of a climatic gradient. At moister sites along this gradient are disturbed upland sites in the subtropical dry to moist forest transition zone indicated by *C. guianensis*, followed by disturbed moist forest of SpaCam and TabHet/CasArb assemblages. This gradient ends in the wet forest assemblage GuaGui/DenArb that was formerly managed for coffee-shade. Another important gradient represents a variation on the preceding one where monthly minimum temperatures, particularly in the spring, differentiate in assemblage distribution.

While similar trends can be seen in the Virgin Islands, there is also an additional separation of *L. leucocephala*-dominated stands and the CorAlb assemblage on St. Croix, which is at a lesser latitude than the other Virgin Islands. Decreasing spring moisture stress, decreasing average monthly temperatures in fall, winter and spring, and increasing in slope and elevation also influence assemblages along this gradient. This gradient ends with the more species-rich dry forest found on St. Thomas. Another Virgin Islands gradient begins with *P. pallida* and *A. farnesiana* assemblages found on flat, highly disturbed areas with less annual precipitation (particularly in the summer and fall months) and moves up into dry–moist transition forests located at higher slope positions. Spring and fall maximum monthly temperatures also played a minor role in assemblage formation and distribution in the Virgin Islands.

Broad ecotones exist on these islands, particularly between the subtropical dry and subtropical moist life zones, and many tree species have equally broad environmental niches along these ecotones. The assemblages are not tightly correlated with specific Holdridge life zones or soil types; rather they tend to occur in multiple life zones and geological parent materials. None of the assemblages were limited to only one life zone, and six assemblages were found in three different life zones. Some assemblages did occur more frequently on certain substrates, but none were restricted to a single substrate, not even those found on ultramafic substrates. Assemblages in the Virgin Islands fit more closely into specific life zones and soil types, but this is probably due to the limited life zones and soil types found on these smaller islands.

4.7. *Land-use history correlations to the species assemblages*

Land-use history can strongly influence tropical forest succession within a climatic zone (Álvarez Ruiz et al., 1997; Rivera and Aide, 1998; Aide et al., 2000; Chinea, 2002; Marcano Vega et al., 2002; Thompson et al., 2007; Abelleira Martínez and Lugo, 2008). When considering differences in species composition across climatic zones, land use and climate are confounded because climate influences land use. In Puerto Rico and the U.S. Virgin Islands, for example, coffee cultivation was limited to moist and wet climatic zones. Sugar cane cultivation occurred in dry and moist zones. Pasture occurs in dry, moist and wet climates. Because these major land uses extend over two or more climatic zones, we conclude that climate is more important to determining variation in species composition across climatic zones than is land-use history. Nevertheless, it still must be recognized that land use and climate are not completely separable.

Several species assemblages were significantly associated with certain geology types or land-use histories in the χ^2 tests but not in the ordinations. The most likely explanation for why land-cover history was not significant here, but was significant in ordinations from other studies, is a combination of the sample design and of the prevalence of certain land covers and trends across mainland Puerto Rico. Most of the forest inventory plots in Puerto Rico were under cultivation for coffee or pasture/herbaceous agriculture before reverting to forest. It follows that the source of most of the variability in our systematic sample is not differences in land use but differences in climate, because the data set in this study span a climate gradient that ranges from very dry forest to cloud forest. In contrast, most other studies, for example, Chinea and Helmer (2003) and Thompson et al. (2002) spanned narrower environmental gradients, such as only humid or only dry climatic zones and two or three geological substrates, and accordingly, land use or geology explains more of the variability in species composition in their plots than in this study. Moreover, in most tree community studies in Puerto Rico, collections of plots were specifically designed to test for differences in land-use or geomorphology by including more equal numbers of plots with different land-use histories. Finally, none of the other studies mentioned use monthly climate data as environmental explanatory variables, which would leave room for more non-climate variables to explain more variation in species composition.

Pasture has been a prominent land cover in Puerto Rico and remains so to this day, because while pasture has reverted to forest at higher elevations, sugar cane has transitioned to pasture in the lowlands (Kennaway and Helmer, 2007). The proportional representation of land-use histories in the mostly systematic sample of inventory plots reflects these land-cover data. In 1951, 41.1% of the points sampled were in pasture, and it has remained a common land cover class until the present day (Table 8). Herbaceous agriculture had largely disappeared from our sample by 1977, and coffee shade by 1991 (Table 10), which is consistent with the findings of Kennaway and Helmer (2007). Of those forest plots where we have mapping data, 35.6% of the forest fell in the 23–49 year old age class. So, while we have data from multiple years for multiple land cover classes, the trends at the majority of the sampled points were all very similar. Additionally, the past land use categories used here might mask a land use that preceded pasture. For example, abandoned herbaceous agriculture might be used as unmanaged pasture before complete abandonment and reversion to forest.

5. Conclusions

The long history of forest disturbance on Puerto Rico and the U.S. Virgin Islands makes it impossible to know precisely how much the currently observed tree species assemblages reflect pre-European colonization forest types and their local variations. However, we know that after large-scale deforestation and forest recovery, at least some novel forests have formed. Naturalized tree species play prominent roles in the recovery and secondary succession of these forests but in differing ways depending on their abilities to regenerate under increasingly closed canopies.

Environmental factors have an overarching effect on forest species composition across the broader range of climatic, geologic and topographic conditions and larger geographic scales, while land-use history also influences subtropical secondary forest species assemblages within a specific climatic zone or set of relatively narrow environmental conditions. More intensive sampling within each land-use history category might be needed to more fully characterize its influence on species composition.

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References

Abelleira Martínez, O.J., Lugo, A.E., 2008. Post sugar cane succession in moist alluvial sites in Puerto Rico. In: Myster, R.W. (Ed.), Post-Agricultural Succession in the Neotropics. Springer, New York, NY, pp. 73–92.

Adam, M.-C., Ryan, C., 2003. Evaluation of Estate Little Princess forest ecosystem: assessment of restoration needs. The Nature Conservancy, Urban and Community Forest Program, Christiansted, St. Croix, p. 26.

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

Aide, T.M., Zimmerman, J.K., Rosario, M., Marcano-Vega, H., 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28, 537–548.

Álvarez Ruiz, M., Acevedo Rodríguez, P., Vázquez, M., 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.

Aukema, J., Carlo, T.A., Collazo, J.A., 2007. Landscape assessment of tree communities in the northern karst region of Puerto Rico. Plant Ecology 189, 101–115.

Bechtold, W.A., Scott, C.T., 2005. The forest inventory and analysis plot design. In: Bechtold, W.A., Patterson, P.L. (Eds.), The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures. General Technical Report SRS-80. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 27–42.

Birdsey, R.A., Weaver, P.L., 1982. The Forest Resources of Puerto Rico. USDA Forest Service Southern Forest Experiment Station, New Orleans, LA, p. 56.

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.

Brandeis, T.J., 2006. Assessing tree species assemblages in highly disturbed Puerto Rican karst landscapes using forest inventory data. Plant Ecology 186, 189–202.

Brandeis, T.J., Helmer, E.H., Oswalt, S.N., 2007. The Status of Puerto Rico's Forests, 2003. USDA Forest Service Southern Research Station, Asheville, NC, p. 75.

Brandeis, T.J., Oswalt, S.N., 2007. The Status of U.S. Virgin Islands' Forests, 2004. USDA Forest Service Southern Research Station, Asheville, NC, p. 61.

Brown, K.A., Scatena, F.N., Gurevitch, J., 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. Forest Ecology and Management 226, 145–152.

Chinea, J.D., 1980. The forest vegetation of the limestone hills of northern Puerto Rico. Master of Science Thesis. Cornell University, Ithaca, NY, p. 69.

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.

Chinea, J.D., Helmer, E.H., 2003. Diversity and composition of tropical secondary forests recovering from large-scale clearing: results from the 1990 inventory in Puerto Rico. Forest Ecology and Management 180, 227–240.

Crowe, T.R., 1980. A rainforest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. Biotropica 12, 42–55.

Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32, 476–498.

Dallmeier, F., Comiskey, J.A., Scatena, F.N., 1998. Five years of forest dynamics following hurricane Hugo in Puerto Rico's Luquillo Experimental Forest. In: Dallmeier, F., Comiskey, J.A. (Eds.), Forest Biodiversity in North, Central and South America and the Caribbean. Research and Monitoring. Parthenon Publishing Group, Washington, DC, pp. 231–248.

Daly, C., Helmer, E.H., Quiñones, M., 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. International Journal of Climatology 23, 1359–1381.

Dansereau, P., 1966. Studies on the Vegetation of Puerto Rico. 1. Description and Integration of the Plant Communities. University of Puerto Rico, Faculty of Arts and Sciences, Institute of Caribbean Science, Mayagüez, Puerto Rico, p. 45.

DuFrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Ewel, J.J., Whitmore, J.L., 1973. The Ecological Life Zones of Puerto Rico and the US Virgin Islands. USDA Forest Service Institute of Tropical Forestry, Río Piedras, Puerto Rico, p. 72.

Francis, J.K., 2000a. Bucida buceras L. Ucar. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de arboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 86–90.

Francis, J.K., 2000b. *Bursera simaruba* (L.) Sarg. Almácigo, gumbo limbo. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de arboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 91–95.

Francis, J.K., 2000c. *Spathodea campanulata* Beauv. Tulipán africano. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 484–487.

Franco, P.A., Weaver, P.L., Eggen-McIntosh, S., 1997. Forest Resources of Puerto Rico, 1990. USDA Forest Service Southern Research Station, Asheville, North Carolina, p. 45.

Freund, R.J., Littel, R.C., 1981. SAS for Linear Models. A Guide to the ANOVA and GLM Procedures. SAS Institute Inc., Cary, NC.

García-Montiel, D.C., Scatena, F.N., 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. Forest Ecology and Management 63, 57–78.

Garrison, L.E., Martin, R.G., Berryhill, H.L., Buell, M.W., Ensminger, H.R., Perry, R.K., 1972. Preliminary Tectonic Map of the Eastern Greater Antilles Region. U.S. Geological Survey, Washington, DC, Miscellaneous Geological Investigations Map I732.

Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M., Tyler, D., 2002. The National Elevation Dataset. Photogrammetric Engineering and Remote Sensing 68, 5–11.

Gould, W.A., González, G., Carrero Rivera, G., 2006. Structure and composition of vegetation along an elevational gradient in Puerto Rico. Journal of Vegetation Science 17, 563–574.

Hatfield, D., 1999. SLOPEPOSITION USDA Forest Service. Pacific Northwest Research Station, Portland, Oregon.

Helmer, E.H., 2004. Forest conservation and land development in Puerto Rico. Landscape Ecology 19, 29–40.

Helmer, E.H., Kennaway, T., Pedreros, D., Clark, M., Tieszen, L., Ruzycki, T., Marcano, H., Schill, S., Carrington, C.M.S., 2008. Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. Caribbean Journal of Science 44, 175–198.

Helmer, E.H., Ramos, O., del Mar-López, T., Quiñones, M., Diaz, W., 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.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15, 1–7.

Kauppi, P.E., Ausubel, J.H., Fang, J., Mather, A.S., Sedjo, R.A., Waggoner, P.E., 2006. Returning forests analyzed with the forest identity. Proceedings of the National Academy of Sciences of the United States of America 103, 17574–17579.

Kennaway, T., Helmer, E.H., 2007. The forest types and ages cleared for land development in Puerto Rico. GIScience & Remote Sensing 44, 356–382.

Krushensky, R.D., 1995. Generalized Geology Map of Puerto Rico. US Geological Survey, Caribbean Division, San Juan, Puerto Rico.

Liegel, L.H., 2000. *Schefflera morototoni* (Aubl.) Maguire. Yagrumo macho. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 465–469.

Little, E.L., Wadsworth, F.H., 1989. Common trees of Puerto Rico and the Virgin Islands. USDA Forest Service, Washington, DC.

Little, E.L., Woodbury, R.O., Wadsworth, F.H., 1974. Trees of Puerto Rico and the Virgin Islands. USDA Forest Service, Washington, DC, p. 1024.

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

Lugo, A.E., Brandeis, T.J., 2005. A new mix of alien and native species coexists in Puerto Rico's landscapes. In: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge University Press, Cambridge, UK, (Chapter 20), pp. 484–509.

Lugo, A.E., Figueroa-Colon, J., Scatena, F.N., 2000. The Caribbean. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, New York, NY, pp. 594–622.

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

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

McCollum, J., 2001. Honeycombing the icosahedron and icosahedroning the sphere. In: Reams, G.A., McRoberts, R.E., Van Deusen, P.C. (Eds.), Proceedings of the Second Annual Forest and Inventory Symposium. General Technical Report SRS-47. USDA Forest Service Southern Research Station, Salt Lake City, Utah, pp. 25–31.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.

McCune, B., Mefford, M.J., 1999.Multivariate Analysis of Ecological Data, PC-Ord Version 4 User's Guide. MjM Software Design, Gleneden Beach, OR.

Molina, S., Alemañy, S., 1997. Species Codes for the Trees of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service, Southern Research Station, Asheville, NC, p. 67.

Molina, S., Lugo, A.E., 2006. Recovery of a subtropical dry forest after abandonment of different land uses. Biotropica 38, 354–364.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Ohmann, J.L., Spies, T.A., 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs 68, 151–182.

Oswalt, S.N., Brandeis, T.J., Dimick, B.P., 2006. Phytosociology of vascular plants on an international biosphere reserve: Virgin Islands National Park, St. John, US Virgin Islands. Caribbean Journal of Science 42, 53–66.

Parrotta, J.A., 2000a. *Acacia farnesiana* (L.) Willd. Aroma, huisache. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 6–10.

Parrotta, J.A., 2000b. *Leucaena leucocephala* (Lam.) de Wit. Leucaena, tantan. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico, pp. 308–316.

Pascarella, J.B., Aide, T.M., Serrano, M.I., Zimmerman, J.K., 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3, 217–228.

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

Ray, G.J., Brown, B., 1995. The structure of five successional stands in a subtropical dry forest, St. John, U.S. Virgin Islands. Caribbean Journal of Science 31, 212–222.

Rivera, L.W., Aide, T.M., 1998. Forest recovery in the Karst region of Puerto Rico. Forest Ecology and Management 108, 63–75.

SAS Institute, 2004. SAS/STAT 9.1 Users Guide. SAS Publishing, Cary, NC.

Silander, S.R., Lugo, A.E., 2000. *Cecropia schreberiana* Miq. Yagrumbo hembra, trumpet-tree. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 122–127.

Skolmen, R.G., 1990. *Prosopis pallida* (Humb. & Donpl. ex Willd.) H.B.K. Kiawe. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America: 2. Hardwoods. Agric. Handbook 654. USDA Forest Service, Washington, DC, pp. 583–586.

Thomas, T., Devine, B., 2005. Island Peak to Coral Reef. A Field Guide to the Plant and Marine Communities of the Virgin Islands. The University of the Virgin Islands, U.S. Virgin Islands.

Thomlinson, J.R., Serrano, M.I., López, T.d.M., Aide, T.M., Zimmerman, J.K., 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica 28, 525–536.

Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham III, E.M., Lodge, D.J., Taylor, C.M., García-Montel, D., Fluet, M., 2002. Land use history, environment, and tree composition in a tropical forest. Ecological Applications 12, 1344–1363.

Thompson, J., Lugo, A.E., Thomlinson, J.R., 2007. Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. Plant Ecology 192, 289–301.

USDA Forest Service, 2002. Field Procedures for Puerto Rico and the Virgin Islands, Supplement C to SRS Regional Manual 1.62. USDA Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit. Accessed June, 2006. Online Manual: http://srsfia2.fs.fed.us/data_acquisition/manual.shtml.

USDA Natural Resource Conservation Service, 2009. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. Accessed June, 2006. On-line database at: http://plants.usda.gov.

Wadsworth, F.H., 1943. Pomarrosa, *Jambos jambos* (L.) Millsp. and its place in Puerto Rico. Caribbean Forester 4, 13–194.

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., 1991. Environmental gradients affect forest composition in the Luquillo mountains of Puerto Rico. Interciencia 16, 142–151.

Weaver, P.L., 1998. Hurricane effects and long-term recovery in a subtropical rain forest. In: Dallmeier, F., Comiskey, J.A. (Eds.), Forest Biodiversity in North, Central and South America and the Caribbean. Research and Monitoring. Parthenon Publishing Group, Washington, DC, pp. 249–270.

Weaver, P.L., 2000a. *Guarea guidonia* (L.) Sleumer. Guaraguao, American muskwood. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 248–254.

Weaver, P.L., 2000b. *Tabebuia heterophylla* (DC.) Britton. Roble blanco, white cedar. In: Francis, J.K., Lowe, C.A. (Eds.), Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. General Technical Report IITF-115. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, PR, pp. 514–518.

Weaver, P.L., 2006a. Estate Thomas Experimental Forest, St. Croix, U.S. Virgin Islands: Research History and Potential. USDA Forest Service International Institute of Tropical Forestry, San Juan, Puerto Rico, p. 62.

Weaver, P.L., 2006b. A Summary of 20 Years of Forest Monitoring in Cinnamon Bay Watershed, St. John, U.S. Virgin Islands. USDA Forest Service International Institute of Tropical Forestry, San Juan, Puerto Rico, p. 35.

Weaver, P.L., Chinea, J.D., 1987. A phytosociological study of Cinnamon Bay watershed, St. John, U.S. Virgin Islands. Caribbean Journal of Science 23, 318–336.

Weaver, P.L., Murphy, E.C., 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22, 69–82.

Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan Publishing Co., Inc., New York.

Woodbury, R.O., Weaver, P.L., 1987. The Vegetation of St. John and Hassel island, U.S. Virgin Islands. U.S. Department of the Interior, National Park Service, Atlanta, GA, p. 101.

Zimmerman, J.K., Pascarella, J.B., Aide, T.M., 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8, 350–360.

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MODELING CARIBBEAN TREE STEM DIAMETERS FROM TREE HEIGHT AND CROWN WIDTH MEASUREMENTS

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ABSTRACT. Regression models to predict diameter at breast height (DBH) as a function of tree height and maximum crown radius were developed for Caribbean forests based on data collected by the U.S. Forest Service in the Commonwealth of Puerto Rico and Territory of the U.S. Virgin Islands. The model predicting DBH from tree height fit reasonably well (R2 = 0.7110), with strongest in subtropical moist and wet forest. The model predicting DBH from crown radius fit the data poorly (R2 = 0.2876), but improvements were made when the model was fit by forest life zone and crown radius measurement protocol. Models fit with both maximum crown radius and tree height had R-square values that ranged from 0.1803 for the subtropical dry forest to 0.8018 for the subtropical moist forest life zone where crown radius was measured with urban forest inventory protocols. Tree heights had stronger correlations with DBH than did crown radius, perhaps due to difficulties in measuring tree crown width or natural variability in this hurricane-disturbed environment. Models that use tree height have some potential for predicting DBH for use in Caribbean forest biomass and carbon estimation models, but the potential for error propagation by using DBH predicted from crown radius is too great to earn our recommendation for such applications.

Keywords: Allometric models; secondary forest; Puerto Rico; U.S. Virgin Islands

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1 INTRODUCTION

Understanding regional and global forest biogeochemical cycles so that informed decisions can be made regarding their management requires accurate estimates of forest structure, biomass and carbon over landscape or larger scales. Direct measurements of forest structure are taken on intensively sampled, relatively small field plots, and these data are used to create allometric models that predict forest parameters like volume, biomass and carbon from easily measured tree attributes. This allows for the expansion of these estimates over greater expanses of forest. Diameter at breast height (DBH) is commonly used as a predictor of other tree metrics in a wide variety of allometric equations. Numerous tree biomass equations use DBH as a predictor variable, with notable examples developed for subtropical and tropical forests [1, 2].

Installation of enough field sampling plots to obtain adequate numbers of DBH measurements is sometimes too costly or difficult in rough terrain or areas that are difficult to access on the ground (e.g. periodic flooding, dense vegetation, etc.), conditions often found in the humid tropics. Estimating DBH from tree metrics that can be measured remotely facilitates landscape and regional scale biomass and carbon estimation. In an early example of this approach, Perez [3] modeled DBH from crown widths measured on aerial photographs in Puerto Rico, Dominica and Thailand. More recent efforts have focused on measuring individual tree heights using lidar data [4-6] or crown widths from high resolution aerial [7] and satellite imagery [8, 9], then using the modeled DBH to estimate total-tree biomass and carbon.

The objective of this study was to develop models to predict tree DBH from tree height and crown radius measurements for Caribbean forest Holdridge life zones [sensu 10] (subtropical dry, subtropical moist, subtropical wet/rain and lower montane) and mangrove forests. The goal was to find models that use variables derived from remotely-sensed data and that would be suitable for estimating tree metrics needed to calculate forest biomass and carbon.

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2 METHODS

2.1 Study area and forest inventories The tree measurements came from two sources: U.S. Forest Service Forest Inventory and Analysis (FIA) forest inventory plots measured in 1980, 1990, and from 2001 to 2004 on the islands of Puerto Rico, Vieques and Culebra in the Commonwealth of Puerto Rico, and on the islands of St. Croix, St. John, and St. Thomas in the Territory of the U.S. Virgin Islands; and U.S. Forest Service Urban Forest Effects (UFORE) inventory plots measured in 2002 in the San Juan Bay Estuary watershed in San Juan, Puerto Rico. The trees measured in FIA plots were in closed canopy stands while those measured on UFORE plots ranged from closed-canopy forest patches to open-grown street and yard trees.

Tree DBH was measured at 1.4 m for all trees with DBH $\geq$ 2.5 cm on both FIA and UFORE plots. On all plots, total tree height (H_T) measurements were taken to the top of the live crown on all live trees with DBH $\geq$ 2.5 cm using a combination of clinometers, Hagloff Vertex III hypsometers, and measurement tapes. Two different protocols, however, were used to measure crown width. On the FIA plots, crown width was recorded to the nearest one-tenth meter by two measurements: longest radius (R_{LONG}) from the bole to drip line and shortest radius (R_{SHORT}) from the bole to drip line, for each live tree with DBH $\geq$ 12.5 cm [for additional tree measurement details see 11]. Crown width on UFORE plots was recorded to the nearest one-tenth meter on trees with DBH $\geq$ 12.5 cm by two measurements: North-South (D_1) and East-West (D_2) widths, drip line to drip line, along the bole [for additional tree measurement details see 12]. In order to make the two datasets as compatible as possible for combined modeling, maximum crown radius (R_{MAX}) was calculated for each set of trees. For the trees measured on the FIA plots, $R_{MAX} = R_{LONG}$. For the trees measured on the UFORE plots,

$$R_{MAX} = \max(D_1/2, D_2/2) \qquad (1)$$

Calculation of R_{MAX} for the UFORE trees assumes that the midpoints of the crown diameters intersect the tree bole. A test of hypothesis H_0: $D_1 = D_2$ was not rejected (p-value = 0.4014) indicating no directional bias, that is, the North-South crown widths were not longer or shorter on average than the East-West widths.

2.2 Model fitting A linear model form was selected for modeling DBH from the predictor variables H_T and R_{MAX}:

$DBH = b_0 + b_1 X_1 + b_2 X_2 + \ldots + b_n X_n$ (2)

We fit models with H_T and R_{MAX} separately, as well as models with both predictor variables together. Additionally, we fit these models by Holdridge life zone to further refine the models with ancillary information that would be commonly available. We used plot center coordinates to extract the Holdridge life zone of each plot from a digitized version of the map that appears in Ewel and Whitmore [10].

Tree DBH and height data were taken from forest inventories conducted in 1980, 1990, and from 2001 to 2004. Only the first measurement of trees that had been measured repeatedly was kept in the dataset. Trees in the Caribbean frequently experience crown and stem damage from hurricanes, and hurricanes Georges (1989) and Hugo (1998) severely damaged forests in Puerto Rico and the U.S. Virgin Islands during the data collection period. We chose to remove trees with damaged stems, tops, or branches noted by the field crew, as opposed to retaining these trees as done in Kenefic and Nyland [13]. Additionally, mean height to diameter ratios were calculated for each tree species. Trees with height to diameter ratios exceeding the mean plus 2 standard deviations were flagged as potential outliers. After further examination of potential outliers in scatter plots, a total of 965 trees were excluded from the data set used to model DBH from H_T.

After the initial model fitting, scatter plots of the residuals were generated. Distribution of the residuals indicated the possible need for a natural log transformation of both H_T and DBH [pages 541-544 in 14]. Since it is well known that the logarithmic transformation results in biased estimates, both transformed and untransformed models were fit to the data. The SAS procedure REG was used to fit the final model of form:

$$\ln(DBH) = b_0 + b_1 \ln(H_T) \qquad (2)$$

or equivalently,

$$DBH = e^{b_0} * H_T^{b_1} \qquad (3)$$

To fit models that predict DBH from crown widths, trees from both the FIA and UFORE plots were included, but the data set was limited to trees most visible in overhead images, that is, trees in the open-grown, dominant, and co-dominant crown classes. After the initial model fitting, scatter plots of the residuals were generated. From these plots, thirteen observations were identified as outliers and subsequently removed from the dataset before the final models were fitted. Note that crown width measurements were made on only a subset of forest inventory plots measured in 2001 to 2004, so this data set is much smaller than the data set used to model DBH from H_T. As previously described, the scatter plots of the residuals resulting from initial model fitting indicated the need for a natural log transformation of both R_{MAX} and DBH. The SAS procedure REG was used to fit the final model of form:

$$\ln(DBH) = b_0 + b_1 \ln(R_{MAX}) \qquad (4)$$

or equivalently,

$$DBH = e^{b_0} * R_{MAX}^{b_1} \tag{5}$$

We then fit models with both H_T and R_{MAX} as predictor variables. This data set was slightly reduced due to missing tree heights for some trees with crown width measurements.

$$\ln(DBH) = b_0 + b_1 \ln(H_T) + b_2 \ln(R_{MAX}) \tag{6}$$

or equivalently,

$$DBH = e^{b_0} * H_T^{b_1} * R_{MAX}^{b_2} \tag{7}$$

3 RESULTS

A total of 13,764 tree measurements taken on FIA plots in all forested life zones found on the islands were used for modeling DBH with H_T (table 1) and 2,739 tree measurements (2,552 forest trees across all life zones and 363 urban inventory trees from the subtropical moist forest life zone only) were used for modeling DBH with R_{MAX} (table 2).

3.1 Models to predict DBH from tree height and crown radius All models predicting DBH from H_T (table 3), R_{MAX} (table 4), and H_T with R_{MAX} (table 5) overall and by Holdridge forest life zone were significant at the 0.05 alpha level. Variation explained by the model with H_T as the sole predictor variable exceeded 71% ($R^2= 0.7110$), and was highest for subtropical wet forest ($R^2= 0.7263$) and lowest for lower montane forests ($R^2= 0.3643$) (table 3).

Models with R_{MAX} as the sole predictor variable explained less variation in DBH (table 4). Variation explained by the model was highest for the lower montane life zone ($R^2= 0.4398$ for models with R_{MAX} alone and 0.4226 for models with R_{MAX} and H_T) and lowest for the subtropical dry forest ($R^2= 0.1575$ and 0.1803). Results indicated that improvements to the subtropical moist forest model, the only life zone with both FIA and UFORE plots, might be possible if fit by crown width measurement protocol. Indeed this was the case as R^2 for the subtropical moist forest UFORE trees improved to 0.7741 from 0.1466 (table 4). The addition of H_T to the R_{MAX} models, however, had little effect on their predictive ability (table 5).

The untransformed model 5b was fit to the data used for model 5a fits. Results (table 6) indicated that all parameter estimates were significantly different from zero with the exception of the height exponent (b_1) for the Mangrove life zone and the FIA protocol. That equation was refit with the height exponent set to zero. Maximum crown radius (R_{MAX}) was replaced with crown area in an attempt to improve model fits, but the resulting fit statistics did not indicate consistent improvement over using R_{MAX}. Total tree height (H_T) was replaced with height above DBH (H_T-1.37) in an attempt to improve estimates of trees just above DBH but again improvement in fit statistics did not warrant modifying the model.

4 DISCUSSION

Many studies have explored the relationship between H_T and DBH [thoroughly reviewed in 15, 16, 17] with the objective of predicting the harder to measure H_T metric from the more easily obtained DBH measurement. Although much of this work has focused on coniferous species, temperate and tropical broadleaf trees also have shown strong H_T and DBH correlations [13, 18, 19] despite their more variable branching patterns and growth forms.

Results of these previous studies show that our models predicting DBH from H_T for Caribbean trees growing in the subtropical moist and subtropical wet forest life zones are of slightly poorer fit than the norm in temperate and tropical hardwood forests, but they still could be used with an understanding of their limitations. Our models for subtropical dry, subtropical lower montane, and mangrove forests, however, are of marginal utility. Variation in DBH explained by H_T was lowest in the subtropical lower montane forest life zone and mangrove forest type. Tree sample size was substantially reduced in these areas. The systematic forest inventory placed few plots in the small, high elevation montane forests and narrow, coastal bands of mangrove forest. Also, the variety of forest types and growth forms within the montane forests, ranging from palms forests to elfin woodlands, complicated fitting of a single model for that life zone.

Although Palace et al. [9] presented an equation to estimate DBH from crown width for tropical forests in the Amazon region (R^2 value of 0.57), it is more common to see studies that present models estimating crown diameter from DBH measurements. Studies show that tree DBH is the best predictor of crown width for both broadleaf and coniferous trees in the continental United States [20-22] and tropical forests in the New World and Old World [3, 8, 9, 23]. The model fits in this study of Caribbean forests, however, generally were poorer than those found in other comparable studies, and the addition of H_T to the models produced only minor improvements in predictive ability. Weaver and Poole [23] fit allometric equations to the relationship between crown diameter and DBH for four species in the Puerto Rican Commonwealth forests subtropical dry (Guánica), subtropical moist (Cambalache), and subtropical wet (Mar-

Table 1: Ranges of the data used to fit Equation 3 by Holdridge life zone.

		DBH				Height, total		
Life zone	N	Mean	Max.	Min.		Mean	Max.	Min.
		- - - - - - *cm* - - - - - -				- - - - - - *m* - - - - - -		
All	13764	12.5	108.6	2.5		8.3	40.0	1.5
Subtropical dry forest	1133	7.4	66.8	2.5		5.5	19.0	1.7
Subtropical moist forest	8829	11.9	105.0	2.5		8.1	37.0	1.5
Subtropical wet forest	3428	15.2	37.0	2.5		9.7	40.0	1.5
Lower montane	286	15.7	69.4	2.5		8.1	22.2	2.0
Mangrove	88	14.9	33.0	2.5		9.8	17.0	2.4

Table 2: Ranges of the data used to fit Equations 4 and 5 by Holdridge life zone and measurement protocol.

			DBH				Height, total				Max. radius		
Life zone	Protocol	N	Mean	Max.	Min.		Mean	Max.	Min.		Mean	Max.	Min.
			- - - *cm* - - -				- - - *m* - - -				- - - *m* - - -		
All	All protocols	2739	21.1	60.0	2.5		12.1	35.1	1.5		3.7	11.1	0.2
	FIA	2552	21.4	60.0	12.5		12.4	35.1	1.5		3.8	11.1	0.2
	UFORE	187	16.8	50.5	2.5		8.6	25.5	1.9		2.6	8.3	0.4
Subtropical moist forest	All protocols	1585	20.8	60.0	2.5		12.0	31.5	1.5		3.7	11.1	0.2
	FIA	1398	19.5	54.7	12.5		8.7	19.0	1.5		3.7	8.6	1.0
	UFORE	187	16.8	50.5	2.5		8.6	25.5	1.9		2.6	8.3	0.4
Lower montane	FIA	115	21.1	57.4	12.5		11.3	22.2	3.0		3.3	8.5	1.0
Subtropical dry forest	FIA	225	19.5	54.7	12.5		8.7	19.0	1.5		3.7	8.6	1.0
Subtropical wet forest	FIA	735	22.3	59.3	12.5		13.6	35.1	2.0		3.9	9.2	0.2
Mangrove	FIA	79	18.9	33.0	12.6		11.4	17.0	4.0		3.2	6.0	1.0

Table 3: Model statistics and parameter estimates from DBH prediction Equation 3a by Holdridge life zone.

		$\ln(DBH) = b_0 + b_1 \ln(H_T)$				
		Model Statistics			Parameter Estimates	
Life zone	N	r^2	RMSE	Pr>F	b_0	b_1
All	13764	0.7110	0.4629	< 0.001	-0.2769	1.2522
Subtropical dry forest	1133	0.5226	0.4757	< 0.001	-0.3123	1.2557
Subtropical moist forest	8829	0.7183	0.4572	< 0.001	-0.3128	1.2602
Subtropical wet forest	3428	0.7263	0.4413	< 0.001	-0.2200	1.2392
Lower montane	286	0.3646	0.5815	< 0.001	0.9809	0.7950
Mangrove	88	0.4822	0.4557	< 0.001	0.4157	0.9727
RMSE = root mean square error						

Table 4: Model statistics and parameter estimates from DBH prediction Equation 4a by Holdridge life zone and tree measurement protocol.

			$\ln(DBH) = b_0 + b_1 \ln(R_{MAX})$				
			Model Statistics			Parameter Estimates	
Life zone	Protocol	N	r^2	RMSE	Pr>F	b_0	b_1
All	All protocols	2791	0.2876	0.3699	< 0.001	2.4071	0.4720
	FIA	2600	0.1796	0.3392	< 0.001	2.5853	0.3410
	UFORE	191	0.7741	0.4023	< 0.001	1.7215	1.0655
Subtropical moist forest	All protocols	1609	0.3183	0.3879	< 0.001	2.3706	0.4945
	FIA	1418	0.1466	0.3337	< 0.001	2.6582	0.2846
	UFORE	191	0.7741	0.4023	< 0.001	1.7215	1.0655
Subtropical dry forest	FIA	225	0.1575	0.2780	< 0.001	2.5452	0.3045
Subtropical wet forest	FIA	746	0.1882	0.3427	< 0.001	2.5906	0.3677
Lower montane	FIA	118	0.4398	0.3071	< 0.001	2.2753	0.6447
Mangrove	FIA	93	0.3458	0.3983	< 0.001	2.0523	0.6723
RMSE = root mean square error							

Table 5: Model statistics and parameter estimates from DBH prediction Equation 5a by Holdridge life zone and tree measurement protocol.

			$\ln(DBH) = b_0 + b_1 \ln(H_T) + b_2 \ln(R_{MAX})$					
			Model Statistics			Parameter Estimates		
Life zone	Protocol	N	r^2	RMSE	Pr>F	b_0	b_1	b_2
All	All protocols	2739	0.3734	0.3229	< 0.001	1.8218	0.3063	0.3229
	FIA	2552	0.2305	0.2971	< 0.001	2.1422	0.2224	0.2391
	UFORE	187	0.8018	0.3639	< 0.001	1.2077	0.7678	0.3723
Subtropical moist forest	All protocols	1585	0.4068	0.3456	< 0.001	1.7754	0.3251	0.3283
	FIA	1398	0.1898	0.3025	< 0.001	2.2790	0.2000	0.1938
	UFORE	187	0.8018	0.3639	< 0.001	1.2077	0.7678	0.3723
Lower montane	FIA	115	0.4226	0.2798	< 0.001	1.9399	0.4700	0.2173
Subtropical dry forest	FIA	225	0.1803	0.2748	< 0.001	2.3566	0.2827	0.1032
Subtropical wet forest	FIA	735	0.3413	0.2849	< 0.001	1.5288	0.2100	0.4868
Mangrove	FIA	79	0.1939	0.2428	0.0003	2.5810	0.3073	-0.0053
RMSE = root mean square error								

Table 6: Model statistics and parameter estimates from DBH prediction Equation 5b by Holdridge life zone and tree measurement protocol.

			$DBH = e^{b_0} * H_T^{b_1} * R_{MAX}^{b_2}$					
			Model Statistics			Parameter Estimates		
Life zone	Protocol	N	r^2	RMSE	Pr>F	b_0	b_1	b_2
All	All protocols	2739	0.3409	7.1465	< 0.001	1.6284	0.4090	0.3272
	FIA	2552	0.2822	7.1187	< 0.001	1.6715	0.4028	0.3039
	UFORE	187	0.7419	6.3029	< 0.001	1.6044	0.2069	0.8123
Subtropical moist forest	All protocols	1585	0.3475	7.2541	< 0.001	1.7145	0.3674	0.3376
	FIA	1398	0.2445	7.2020	< 0.001	1.8163	0.3475	0.2948
	UFORE	187	0.7419	6.3029	< 0.001	1.6044	0.2069	0.8123
Lower montane	FIA	115	0.4826	7.1210	< 0.001	1.4340	0.3983	0.5585
Subtropical dry forest	FIA	225	0.2057	6.2519	< 0.001	2.1023	0.1714	0.3983
Subtropical wet forest	FIA	735	0.3707	7.0686	< 0.001	1.0804	0.6513	0.2543
Mangrove	FIA	79	0.1893	4.9000	< 0.001	2.5657	0	0.3359
RMSE = root mean square error								

icao) forest life zones with an overall R^2 value of 0.795. Perez (1970) also modeled crown diameter by DBH for trees in Puerto Rico and Dominica but did so based on the means of 10-cm diameter classes rather than on the DBH of the individually measured trees. By doing so, tree allometric variation was reduced resulting in uncommonly high R^2 values of 0.8510 to 0.9898 that are not analogous to the results of this or other studies cited herein. Bechtold [20] presented species-specific models predicting crown width based on DBH for 66 broadleaf species in temperate forests in the eastern U.S. R-square values ranged between 0.13 and 0.88 across all 66 species, with 36 species having R^2 values greater than or equal to 0.5.

There were substantial differences in our model fits by measurement protocol, with models fit to the UFORE data generally being much better than those fit to the FIA data. This could be for two reasons, the first biological and the second procedural. First, the urban forest trees in the UFORE data could possibly have more symmetrical, less variable crowns than their closed forest counterparts measured on the FIA plots. Basal areas on the UFORE plots ranged from 1.2 to 5.3 m^2/ha with an average of 3.1 m^2/ha (unpublished data), whereas basal areas on the FIA plots ranged from 8 to 26 m^2/ha with an average of 19 m^2/ha in Puerto Rico [24], and from 10 to 19 m^2/ha with an average of 13 m^2/ha for the U.S. Virgin Islands ..25]. Less competition on the UFORE plots allows the trees to grow fuller, more symmetrical crowns that are more amenable to modeling. Secondly, the FIA protocol called for the specific measure of the longest crown radius whereas the UFORE protocol measured along the cardinal directions with no regard for which part of the crown was widest or narrowest. Only by random chance would the longest axis of the crown be measured by the UFORE protocol and therefore, the variation in R_{MAX} for any given DBH was inherently smaller among the UFORE trees than among the FIA trees. On the FIA plots, variation in R_{LONG} may be exaggerated by the inclusion of atypically long, stray branches growing toward canopy gaps.

Modeling broadleaf tree crowns, particularly in the tropics, is complicated by the inherently high variability in crown width. In addition to the usual stand competition factors present in all forests, subtropical Caribbean forests experience hurricanes with sufficient frequency that trees potentially have their crowns damaged multiple times during their lifetime. This likely produces crowns that are reduced in size and more irregular for a given DBH than trees undamaged by hurricanes ....3]. Although we made every effort to exclude damaged stems and crowns from the data set, influential damages from the past are not always evident. The extent to which variability was compounded by past damage and the crown width measurement protocols is unknown. The crown width measurement protocols with which our data were collected was unlike that in other similar studies, i.e., that of using the average of two diameters, the first measured at the widest point of the crown and the second measured perpendicular to, and bisecting, the first [20, 21, 23, 26-28]. Perhaps variation would have been reduced, particularly for the FIA trees, had the data been collected in this more common manner.

It should also be remembered that models to estimate DBH from remotely-sensed crown and tree height measurements could potentially differ from models built using ground-based measurements and introduce additional sources of error. Asner et al. .8] describe the difficulties of estimating crown width from IKONOS imagery. Their satellite image-based crown area estimates were an average of 65% greater than field measurements.

5 CONCLUSIONS

Models that use a field or remotely-sensed measurement of H_T as a predictor variable can be expected to produce a reasonably accurate estimate of DBH in Caribbean subtropical moist and subtropical wet forest, but these estimates should only be used with an understanding of their limitations. Models that use a crown width measurement such as R_{MAX} are sensitive to field data collection methods and suffer from the variability inherent in tree crowns. With most R^2 values falling below a reasonably moderate level of correlation, the potential for error propagation from using a DBH predicted from R_{MAX} measurements in Caribbean forest biomass and carbon estimation models, as has been attempted for some Amazonian forests ..8, 9], is too great to earn our recommendation. While we would like to see the predictive capabilities of these models improved, we do not think that more data should necessarily be collected with the crown width measurement protocols employed here. We expect the use of other measurement protocols, such as measuring multiple radii from the bole to the drip line or measuring the longest diameter drip line to drip line and a perpendicular width, might provide data more amenable for modeling purposes. Therefore, we recommend further study of crown width measurement protocols to determine if indeed the irregular crowns of Caribbean forest species can be predicted with acceptable levels of accuracy. Also, we recommend that models that predict DBH from remotely-sensed crown and height measurements be developed for comparison to models derived from ground-based measurements.

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REFERENCES

Asner,G.P., M. Palace, M. Keller, R. Pereira, and J.N.M. Silva. 2002.Estimating canopy structure in an Amazon forest from laser range finder and IKONOS satellite observations. Biotropica 34(4), pp. 483-492.

Bechtold, W.A. 2003. Crown-diameter prediction models for 87 species of stand-grown trees in the Eastern United States. Northern Journal of Applied Forestry 24(4):269-278.

Bechtold, W.A. 2004. Largest-crown-width prediction models for 53 species in the western United States. Western Journal of Applied Forestry 9(4):245-251.

Brandeis, T.J., E.H. Helmer, and S.N. Oswalt. 2007. The status of Puerto Rico's forests, 2003. USDA Forest Service Southern Research Station, p. 75.

T.J. Brandeis and S.N. Oswalt. 2007. The Status of U.S. Virgin Islands' Forests, 2004. USDA Forest Service Southern Research Station 61 p.

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 55 p.

Brown, S., T. Pearson, D. Slaymaker, S. Ambagis, N. Moore, D. Novelo, and W. Sabido. 2005. Creating a virtual tropical forest from three-dimensional aerial imagery to estimate carbon stocks. Ecological Applications 15(3): 1083-1095.

Chave,J., C. Andalo, S.L. Brown, M.A. Cairns, J.Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira, J.P. Lescure, B.W. Nelson, H. Ogawa, H. Puig, B. Riéra, and T. Yamakura. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87-99.

Cole, T.G. and J.J. Ewel. 2006. Allometric equations for four valuable tropical tree species. Forest Ecology and Management 229:351-360.

Colbert, K.C., D.R. Larsen, and J.R. Lootens. 2002. Height-diameter equations for thirteen Midwestern bottomland hardwood species. Northern Journal of Applied Forestry 19(4):171-176.

Curtis, R.O. . 1967. Height-diameter and height-diameter-age equations for second-growth Douglas-fir. Forest Science 13(4):65-375.

Ewel, J.J. and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the US Virgin Islands. USDA Forest Service Institute of Tropical Forestry, 72 p.

Falkowski, M.J., A.M.S. Smith, A.T. Hudak, P.E. Gessler, L.A. Vierling, and N.L. Crookston. 2006. Automated estimation of individual conifer tree height and crown diameter via two-dimensional spatial wavelet analysis of lidar data. Canadian Journal of Remote Sensing 32(2):153-161.

Francis, J.K. 1988. The relationship of bole diameters and crown widths of seven bottomland hardwood species. Southern Forest Experiment Station. Research Note SO-328 3 p.

Huang S., and S.J. Titus. 1994.An age-independent individual tree height prediction model for boreal spruce-aspen stands in Alberta. Canadian Journal of Forest Research 24:1295-1301.

Kenefic, L.S., and R.D. Nyland. 1999. Sugar maple height-diameter and age-diameter relationships in an uneven-aged northern hardwood stand. Northern Journal of Applied Forestry 16(1): 43-47.

Larocque, G.R., and P.L. Marshall. 1994. Crown development in red pine stands. I. Absolute and relative growth measures. Canadian Journal of Forest Research, Vol. 24, pp. 762-774.

Martin, F.C., and J.W. Flewelling. 1998. Evaluation of tree height prediction models for stand inventory. Western Journal of Applied Forestry 13(4):109-119.

Nowak, D.J., D.E. Crane, J.C. Stevens, and R.E. Hoehn. 2005. The urban forest effects (UFORE) model: Field data collection manual. USDA Forest Service, Northern Research Station 34 p.

Palace, M., M. Keller, G.P. Asner, S. Hagen, and B. Braswell. 2008. Amazon forest structure from IKONOS satellite data and the automated characterization of forest canopy properties, Biotropica 40(2):141-150.

Perez,J.W.. 1970. Relation of crown diameter to stem diameter in forests of Puerto Rico, Dominica, and Thailand. In: A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico, R.F. Pigeon, Editor, Division of Technical Information, U.S. Atomic Energy Commission, pp. 105-122.

Popescu, S.C. 2007. Estimating biomass of individual pine trees using airborne lidar. Biomass and Bioenergy, 31: 646-655.

Popescu, S.C., R.H. Wynne, and R.F. Nelson. 2003. Measuring individual tree crown diameter with lidar and assessing its influence on estimating forest volume and biomass. Canadian Journal of Remote Sensing, Vol. 29(5):564-577.

Smith, W.R., R.M. Farrar Jr., P.A. Murphy, and J.L. Yeiser. 1992. Crown and basal area relationships of open-grown southern pines for modeling competition and growth. Canadian Journal of Forest Research 22:341-347.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. Second ed, W.H. Freeman and Company 859 p.

USDA Forest Service. 2006. Forest Inventory and Analysis National Field Manual. Volume 1. Field Data Collection Procedures for Phase 2 Plots. Caribbean Version 3.0., http://www.srs.fs.usda.gov/fia/data_acquisition/-field_guide/Final/SRS_Caribbean_Ver_3_2006.pdf.

Weaver, P.L., and D.J. Pool. 1979. Correlation of crown features to growth rates in natural forests of Puerto Rico. Turrialba 29(1), pp. 53-58.

Zarnoch, S.J., W.A. Bechtold, and K.W. Stolte. 2004. Using crown condition variables as indicators of forest health. Canadian Journal of Forest Research, 34:1057-1070.

Thomas J. Brandeis and Christopher W. Woodall

Assessment of Forest Fuel Loadings in Puerto Rico and the US Virgin Islands

Quantification of the downed woody materials that comprise forest fuels has gained importance in Caribbean forest ecosystems due to the increasing incidence and severity of wildfires on island ecosystems. Because large-scale assessments of forest fuels have rarely been conducted for these ecosystems, forest fuels were assessed at 121 US Department of Agriculture forest service inventory plots on Puerto Rico, Vieques, and the US Virgin Islands. Results indicated that fuel loadings averaged 24.05 Mg ha^{-1} in 2004–2006. Forest litter decreased from wetter to drier forest life zones. These island forests showed a paucity of coarse woody fuels (CWD) (2.91 Mg ha^{-1}) and relatively greater quantities of smaller-sized fine woody fuels (FWD) (10.18 Mg ha^{-1} for FWD and 10.82 Mg ha^{-1} for duff/litter) when compared to continental tropical forests. Between 2001 and 2006, CWD fuel loads decreased, while fine fuels and litter increased, such that total fuel loads remained constant on a subset of plots on Puerto Rico. This trend indicates that continued decomposition of CWD deposited by the last severe hurricane is balanced by increasing inputs of FWD from recovering and maturing secondary forests. Forest disturbance cycles and successional development must be taken into account by agencies charged with fire protection and risk assessment.

INTRODUCTION

In the absence of human activities, wildfires are an infrequent event in Caribbean forests (1). The increasing frequency of wildfires related to agricultural burning, arson, and human carelessness has increased concern about these effects on forest tree species composition and structure, particularly the islands' subtropical dry forests (1, 2). Wildfires can heavily impact island ecosystems, sometimes maintaining extensive areas of young forest in a suspended successional state, impairing the delivery of ecosystem services, and slowing forest recovery processes. Forested watersheds retain more freshwater and stabilize soils, and so maintain the health of tightly linked Caribbean terrestrial and marine ecosystems. Island economies benefit from recreational and ecotourism benefits created by these uniquely biodiverse Caribbean forests.

Although Caribbean island forest ecosystems are influenced by hurricane disturbances (3–9), the additional anthropogenic disturbance of wildfires may represent a tipping point in some indigenous forest ecosystems. Chronically burned Caribbean forests may no longer support their notably high levels of biodiversity and endemism (10), an ecosystem attribute that may never be attained again. For example, fires favor tree species that have adapted to survive them, such as *Leucaena leucocephala* (Lam.) De Wit. (11). These trees often survive fires by resprouting, similar to what occurs after cutting (12) or hurricane damage (13). Some tree species' seeds survive in the soil seed bank until competing vegetation is killed, after which they create dense stands of small, multistemmed trees and shrubs.

Fire is also of growing concern in Caribbean ecosystems due to increased economic losses and risks to local populations. As island human population densities increase, it is likely that losses from uncontrolled wildfires will increase. Firefighting public agencies will be hard-pressed to meet the demand for fire suppression and structure protection activities as wildfires occur more frequently in the growing, increasingly complex, wildland-urban interface.

The situation in the Caribbean is a microcosm of the continental United States, where increasing fire frequency, severity, greater economic losses, and firefighting costs have created a demand for better wildfire fuel load estimates, fuel models, and risk assessments. Because downed woody materials (DWM) such as coarse and fine woody debris (CWD and FWD, respectively) are a major determinant of wildfire behavior, quantification of these fuels in a spatially explicit manner allows land managers to properly assess fire hazards. To inform such decision-making processes, forest fuels that increase wildfire risks must be assessed. However, obtaining the data necessary to estimate fuel loads and fire behavior requires extensive ground-based sampling across the landscape (14).

The need for fuel loading information across the United States guided the incorporation of DWM measurement protocols into the US Forest Service's Forest Inventory and Analysis (FIA) program in the United States beginning in 2001 (Puerto Rico in 2000–2001, US Virgin Islands in 2004). Estimates of downed woody fuels, combined with standing-tree fuel information from the standard forest inventory, recently presented for Puerto Rico in Brandeis, Helmer, and Oswalt (15) and for the US Virgin Islands presented in Brandeis and Oswalt (16), can provide much of the information needed for wildfire risk assessment.

The main objective of this study was to estimate mean fuel loadings (biomass) for forests in Puerto Rico and the US Virgin Islands according to fuel size classes: FWD (1 hr, 10 hr, 100 hr time lags), CWD (1000+ hr time lag), duff, and litter (17). Additionally, mean fuel loadings by forested life zones were compared to further identify areas of higher risk. Changes in fuel loadings in relation to forest maturation and disturbance events were assessed using estimates of fuel loading over a 5 y period on mainland Puerto Rico. Finally, study results were examined in a regional and global context using published literature for comparable DWM studies in tropical and temperate forests.

MATERIALS AND METHODS

Study Area and Sampling Design

Data used in this study were derived from FIA inventories from Puerto Rico (including Vieques) and the US Virgin Islands. These data were collected at sampling points along a computer-generated hexagonal grid spread evenly across the islands, providing an unbiased, systematic DWM sampling framework (18). Initially, 25 plots were installed systematically in 2001 on mainland Puerto Rico. The inventory was extended to include Vieques and the US Virgin Islands in 2004. In 2006, sampling intensity was increased on mainland Puerto Rico to increase

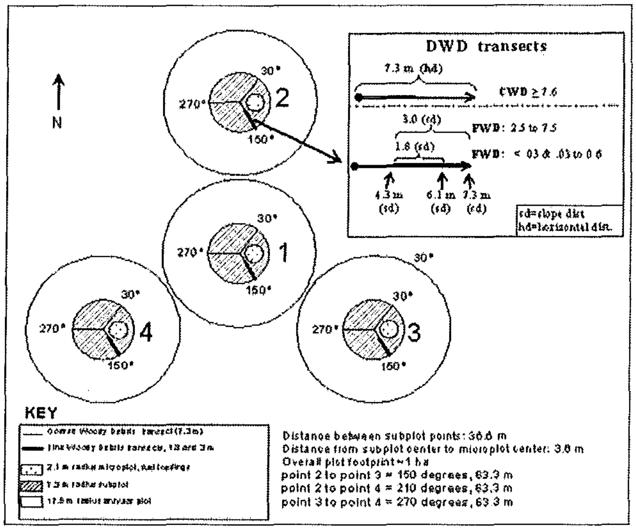

Figure 1. US Forest Inventory and Analysis plot layout. (Adapted from Woodall and Williams [24].)

precision and include lower montane forest (19, 20). Data from a total of 121 plots were used for this study, 93 in Puerto Rico (90 mainland, 3 Vieques) and 28 in the Virgin Islands (7 on St. Croix, 20 on St. John, and 1 on St. Thomas). The initial 25 plots on mainland Puerto Rico were measured twice (2001 and 2006). Plots were stratified by island and Holdridge life zone according to a digitized version of the life zone map published by Ewel and Whitmore (21).

Fuel Categories and Measurements

FIA inventory plots consist of a cluster of four subplots (Fig. 1). Detailed information on plot location, installation, marking, site descriptions, tree measurement, tree damage description, and other data collected at each forested plot can be found in Bechtold and Scott (22) and the US Department of Agriculture (USDA) Forest Service (23). Forest fuels are the organic matter available for fire ignition and combustion (14), and they are commonly quantified by size/hour classes that reflect the time required for their moisture content to change significantly (24). For the purposes of this study, CWD was defined as dead and downed (greater than 45° lean from vertical) woody material with a diameter of at least 8 cm at its point of intersection with a sampling transect and at least 1 m in length. CWD (Table 1) was sampled on three 7.3-m-long transects radiating from each FIA subplot center at 30°, 150°, and 270° (24). Several attributes were measured for each CWD piece: transect diameter (diameter of piece where it crosses the transect), total length, small-end diameter, large-end diameter, decay class, species, evidence of fire, and presence of cavities. This study defined FWD as downed and dead woody material below 8 cm in size at its point of intersection with a sampling transect. FWD was sampled only along the 150° transect on each subplot in three size classes (Table 1). One (transect diameter less than 0.6 cm) and 10 hr fuels (transect diameter between 0.6 and 2.4 cm) were sampled along 1.8 m of the 150° transect, and 100 hr fuels (transect diameter between 2.5 and 7.6 cm) were sampled along 3 m of the 150° transect (Table 1). Duff (defined as decomposing leaves and other organic material containing no recognizable plant parts) and litter (loose plant material found on the duff surface, not including bark or elements that meet the definitions of FWD or CWD) depths were measured within a 30-cm-diameter sampling frame at the ends of each 7.3 m transect.

Table 1. Downed woody material (DWM) classes, fuel-hour classes, diameter classes (cm), and sampling transect slope lengths (m). (Adapted from Woodall and Williams [24].)

DWM class	Fuel-hour	Diameter	Transect length
Small fine	1	0.03–0.6	1.8
Medium fine	10	0.6–2.4	1.8
Large fine	100	2.5–7.6	3
Coarse	1000+	7.6+	7.3

Estimation and Analysis

Fuel loadings per plot (totals and by fuel category subsets) were estimated using line intersect models (24–26). For further information regarding the FIA sample protocol and estimation procedures for DWM, see Woodall and Williams (24). Comparisons of mean fuel values between life zones were made for the two measurement periods (2001 and 2004–2006) separately in order not to confound difference between life zones with change over time. The plots measured in 2001 were located only on mainland Puerto Rico. The plots measured in 2004–2006 were on Vieques (2004), the US Virgin Islands (2004), and mainland Puerto Rico (2006). The reasons for this division were: *i*) to have two measurement periods for estimating fuel loading changes on mainland Puerto Rico; and *ii*) to assess the current fuel loadings across all the islands.

Mean life zone values were compared for statistically significant differences ($\alpha \leq 0.05$) using the SAS Version 8.0 PROC GLM procedure of analysis of variance with a model of less than full rank and least-squares means comparisons (27). Analyses of change in fuel loadings on mainland Puerto Rico were made using only the data collected in 2001 and 2006. All data collected in 2006 were used, even from plots that were not measured in 2001, because the extra data provided superior estimates of DWM and fuels at the second measurement period. Change estimates were made using the PROC MIXED procedures for repeated measures, where the autoregressive covariance structure was chosen after examination of the REML log likelihood, Akaike Information Criterion, and Schwarz Bayesian Criteria statistics (28). For all means comparisons, an alpha level of 0.05 was used for establishing statistical significance.

One plot measured in 2006 in the subtropical dry forest had CWD biomass (88.79 Mg ha^{-1}) that was much higher than any other plot due to four large fallen logs, one with transect diameter of 70 cm. Trees with a diameter at breast height (d.b.h.) >60 cm are uncommon in the forests of Puerto Rico (15). The data point from this single plot was strongly influential in increasing the mean value for that life zone and the entire measurement year. While the data point from this plot can be seen as representing the high variability of DWM across the forest landscape, it was excluded from further analysis.

Conversely, one of the two plots in the mangrove forest showed the highest observed amounts of duff (46.97 Mg ha^{-1}), but those data were retained. This was done for two reasons. First, plots in other life zones had duff amounts that approached this high value. Second, there were only two plots in mangrove forest, and dropping the data from one would have further weakened estimates for that forest type. The reader should keep in mind the small sample sizes for mangrove and lower montane forest when interpreting the following results.

RESULTS

Fuel Loadings

Some mean CWD, FWD, duff, and litter fuel loads varied significantly from one measurement period to the next (Table

Table 2. Mean values for woody and forest floor fuels (in Mg ha^{-1}, with standard errors of the mean) for Puerto Rico and the US Virgin Islands. Results are presented for measurement periods 2001, 2004–2006, and both measurement periods combined. The p values are from means comparisons tests between the two measurement periods.

Fuel class	Mean 2001 (N = 25)	Mean 2004–2006 (N = 121)	p	Mean all years (N = 146)
1 hr	0.70 (0.11)	1.30 (0.12)	0.0019	1.20 (0.093)
10 hr	4.98 (0.49)	3.73 (0.34)	0.2341	3.94 (0.30)
100 hr	6.45 (1.112)	5.15 (0.58)	0.5796	5.37 (0.52)
Subtotal fine woody fuels	*12.13 (1.35)*	*10.18 (0.85)*	*0.6419*	*10.51 (0.74)*
1000+ hr	11.17 (2.71)	2.91 (1.28)	0.0431	4.33 (1.18)
Subtotal all woody fuels	*23.29 (3.17)*	*13.10 (1.63)*	*0.1196*	*14.84 (1.48)*
Duff	8.07 (1.51)	3.82 (0.86)	0.1367	4.55 (0.77)
Litter	4.57 (6.53)	7.00 (0.67)	0.0458	6.58 (0.77)
Subtotal forest floor fuels	*12.63 (1.83)*	*10.82 (12.4)*	*0.8928*	*11.13 (1.08)*
Total fuels	**34.17 (3.54)**	**24.05 (2.28)**	**0.3909**	**25.78 (2.00)**

2), and these differences varied by life zone. There were no differences in quantities of fuel loadings between life zones in the data collected only in 2001 on mainland Puerto Rico. (Note that the lower montane life zone was not sampled in 2001.) However, in the second measurement period, there were differences in the total fuels ($p = 0.0014$) (Fig. 2), duff ($p < 0.0001$), and litter ($p < 0.0001$) between life zones. Subtropical dry (14.92 Mg ha^{-1}) and moist (22.13 Mg ha^{-1}) forests had fewer tons of fuels than values found in subtropical wet (36.95 Mg ha^{-1}) and mangrove (63.85 Mg ha^{-1}) forests (Fig. 2). Neither CWD nor FWD differed significantly between life zones for this measurement period (Fig. 3).

The differences between life zones were due to the organic material found on the forest floor (Fig. 4). The amount of duff found in the two mangrove forest plots was striking and significantly greater (38.28 Mg ha^{-1}, all $p < 0.05$) than values found in any other life zone. Otherwise, duff amounts did not vary greatly by life zone except for subtropical wet forest (6.35 Mg ha^{-1}), which had greater amounts of duff than values found in subtropical dry forest (1.41 Mg ha^{-1}, $p = 0.0251$). Litter amounts, however, clearly decreased as the life zones became drier. Subtropical dry forests had less litter (3.54 Mg ha^{-1}) than lower montane (19.24 Mg ha^{-1}, $p = 0.0013$) and subtropical wet (12.76 Mg ha^{-1}, $p < 0.0001$) forests, and somewhat less than subtropical moist forests (6.27 Mg ha^{-1}, $p = 0.0551$). Mangrove forest litter amounts were relatively low (2.72 Mg ha^{-1})—significantly lower than values found in lower montane ($p = 0.0128$) and subtropical wet forests ($p = 0.0386$). Again, the very small lower montane and mangrove forest sample sizes must be taken into consideration when interpreting these results.

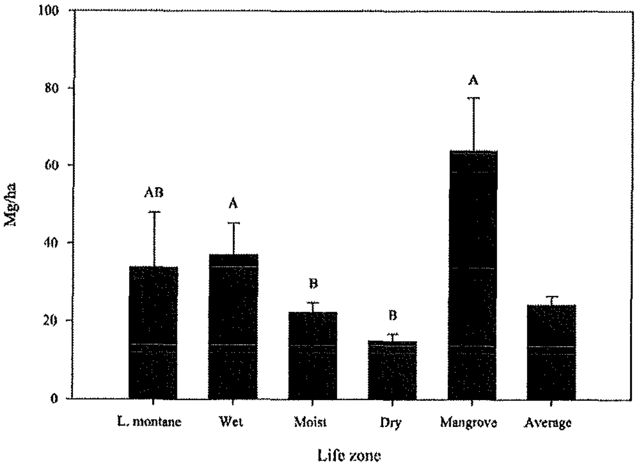

Figure 2. Total amounts of potential forest fire fuels (sum of all 1000+ hr, 100 hr, 10 hr, and 1 hr fuels, plus forest floor litter and duff in Mg ha^{-1}) for Puerto Rico and the US Virgin Islands as measured in 2004–2006, by forest life zone and average value across all life zones, with standard error of the mean. Note that the number of plots in each life zone is indicated at the base of each bar.

Change in Fuel Loadings Over Time

FWD, CWD, and the forest floor fuel loads changed significantly over the 5 y measurement period on mainland Puerto Rico (Table 2). There were increases in the smallest category of FWD, the 1 hr fuels ($p = 0.0019$), and in amounts of litter ($p = 0.0458$). Conversely, CWD, the largest-sized fuel category, decreased ($p = 0.0431$). Despite these changes, total fuels per hectare did not change significantly, and levels of the other individual fuel categories remained relatively steady.

DISCUSSION

Fuel Loadings in a Regional and Global Context

The regional context for these baseline measurements is made difficult by the differences in sampling protocols and definitions used in other published studies. As such, for valid comparisons, this study's results have been summarized by varying detrital categories utilized in a diversity of other studies in Puerto Rico and other tropical/temperate forests (Table 3). In Puerto Rico, Li et al. (29) found 5.9 Mg ha^{-1} of total forest floor mass, which is described as both litter and downed wood, in secondary forest in the Luquillo Mountains. This amount of fuels is much lower than the 36.95 Mg ha^{-1} for subtropical wet forest and 33.7 Mg

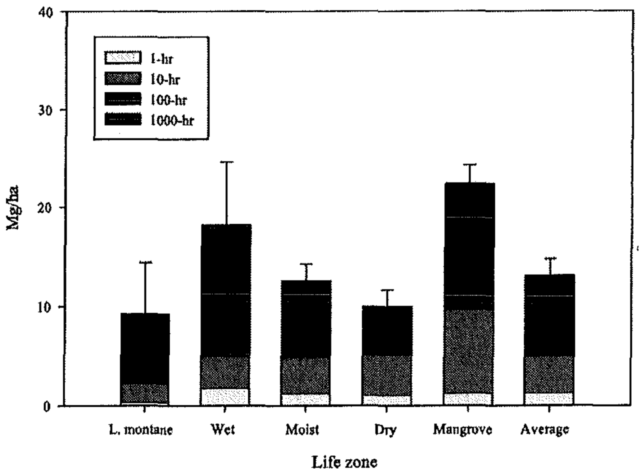

Figure 3. Forest fire fuels (Mg ha^{-1}) by piece size category for Puerto Rico and the US Virgin Islands by forest life zone and averaged across all life zones, with standard error of the total mean value.

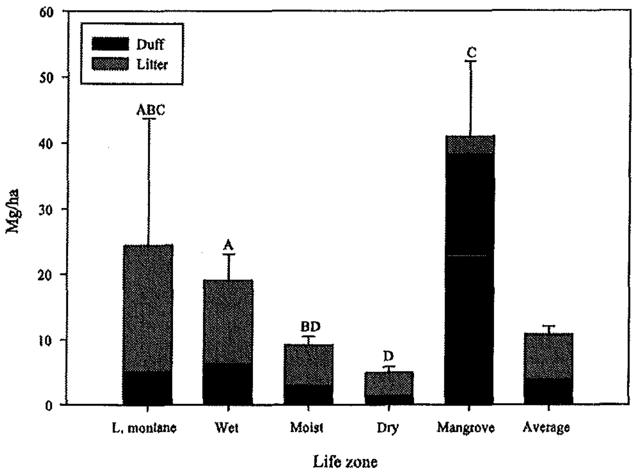

Figure 4. Forest floor litter and duff (Mg ha^{-1}) for Puerto Rico and the US Virgin Islands by forest life zone and averaged across all life zones, with standard error of the total mean value. Letters indicate significant differences between mean total values.

ha^{-1} for lower montane forest found by this study in the two forest types that would occur in that area. Similarly, the subtropical wet forest mean litter and FWD mean value of 22.51 Mg ha^{-1} found by the current study is much higher than the 13.3 Mg ha^{-1} of litter and FWD estimated by Lugo et al. (30) for secondary forest in Barranquitas, Puerto Rico. Murphy and Lugo (31) found 2.7 Mg ha^{-1} of FWM and CWM, and 12.3 Mg ha^{-1} of leaf litter in the Guánica Commonwealth forest in Puerto Rico. The current study found 9.39 Mg ha^{-1} of FWM and CWD in subtropical dry forest and only 3.54 Mg ha^{-1} in leaf litter.

On a regional and global scale, it appears that the amounts of fuels, particularly CWD, in forests of Puerto Rico and the US Virgin Islands fall at the lower end of observed values for other tropical and temperate forests. Average CWD values for tropical wet and moist forests in South and Central American tropical forests range from 16.7 Mg ha^{-1} (32, for Venezuelan moist forest) to 46.3 Mg ha^{-1} (33, for La Selva, Costa Rica) (Table 3), which are well above even the higher averages from the Puerto Rico measurements taken in 2001 of 12.16 Mg ha^{-1} for subtropical moist forest and 12.18 Mg ha^{-1} for subtropical wet forests. The current study's CWD results fell within, but at the low end, of the widely varying range of values observed in temperate hardwood forests. Although there were fewer studies with comparable forest floor measurements, litter and duff amounts found here were also lower, but similar, to other tropical forests (Table 3).

The smaller-sized FWD fuels, however, appear to be present in greater quantities on Puerto Rico and the US Virgin Islands (Table 3), and the difference between the island forests and continental tropical forests increases with increasing moisture and potentially greater site productivity. Delaney et al. (32) found 2.4 Mg ha^{-1} of CWD and 5.2 Mg ha^{-1} of FWD in Venezuelan dry forest, values that are similar to the 0.57–1.21 Mg ha^{-1} of CWD and 7.04–9.40 Mg ha^{-1} of FWD found in subtropical dry forest by the current study for the two measurement periods. However, the Venezuelan lower montane moist and wet forest held 17.2–21.2 Mg ha^{-1} of CWD and 2.7–3.1 Mg ha^{-1} of FWD, while Puerto Rican lower montane forest held only 5.33 Mg ha^{-1} of CWD and 3.92 Mg ha^{-1} of FWD. We cannot yet make any assertions regarding fuel loading trends until sample sizes are increased along with more comparable studies from other regions.

Forest Fuel Dynamics, Disturbance, and Forest Maturation

The rather static value of total tons of fuels per hectare over the past 5 y is due to increases in FWD and decreases in CWD. Lugo and Scatena (45) noted that leaf fall and litter production remained very constant over a 25 y observation period, but they attributed this stability to the age of the relatively mature tabonuco forest they studied. Secondary forests and plantations within the same experimental forest showed much more variation, and tendencies toward increasing leaf fall with age (45). Increasing litterfall, and with it increasing FWD, would seem to be a logical phenomenon in stands in early stages of stand development, where crown development, branch shedding, and canopy closure occur at a relatively rapid rate compared to latter stages of stand development (46). Forest age and structural development might also help explain the relative paucity of larger-sized fuels found in Puerto Rico and the US Virgin Islands. Almost all of the islands' forests and the sites sampled, except possibly in the lower montane life zone, are still

Table 3. Values (Mg ha^{-1}) of coarse woody debris (CWD), fine woody debris (FWD), forest floor (sum of litter and duff), and total downed woody materials (DWM) observed in this study and comparable published studies. Note that total DWM from this study does not sum exactly due to rounding.

Location	CWD	FWD	CWD and FWD	Forest floor	Total DWM	Source
Puerto Rico, wet forest	–	–	–	–	5.9	Li et al. 2005 (29)
Puerto Rico, wet forest	–	–	–	–	11.0–16.0	Lugo et al. 1999 (30)
Puerto Rico, dry forest	–	–	2.7	12.3	–	Murphy and Lugo 1986 (31)
Venezuela, dry forest	2.4	5.2	7.6	–	–	Delaney et al. 1997 (32)
Venezuela, dry/moist transition	3.3	2.7	6.0	–	–	Delaney et al. 1997 (32)
Venezuela, lower montane moist	21.2	3.1	24.3	–	–	Delaney et al. 1997 (32)
Venezuela, lower montane wet	17.2	2.7	19.9	–	–	Delaney et al. 1997 (32)
Venezuela, moist forest	16.7	2.4	19.1	–	–	Delaney et al. 1997 (32)
Costa Rica, La Selva	46.3	–	–	–	–	Clark et al. 2002 (33)
Mexico, moist forest	–	–	0–14	2.1–7.7	–	Hughes, Kauffman, and Jaramillo 1999 (34)
Mexico, dry forest	5.3–31.5	3.5–6.0	–	–	–	Eaton and Lawrence 2006 (35)
Brazil, Amazon	28.9	9.6	38.5	–	–	Cummings et al. 2002 (36)
Brazil, Amazon	24.7	3.2	27.9	7.6	63.4	Nascimento and Laurance 2002 (37)
Guyana, rain forest	21.5–22.6	2.9	–	–	–	ter Steege 2001 (38)
Slovenia, temperate forest	40.0–179.3	–	–	–	–	Debeljak 2006 (39)
US, temperate forest	4.4	7.3	11.7	17.9	32.0	Chojnacky and Schuler 2004 (40)
US, temperate forest	39.8–137.2	–	–	–	–	Idol et al. 2001 (41)
US, temperate forest	2.2–158.4	–	–	–	–	Rubino and McCarthy 2003 (42)
US, all forest	–	–	–	–	10.2–88.8	Birdsey 1992 (43)
Ecuador, montane forest	–	–	–	–	11.0–12.7	Fehse et al. 2002 (44)
Puerto Rico and US Virgin Islands	**4.3**	**10.5**	**14.8**	**11.1**	**25.8**	**This study**

at a young, vigorously growing developmental stage (15), so there is little natural mortality that would leave large logs on the ground. Most of the published studies cited here were in more mature forest. Hughes, Kauffman, and Jaramillo (34) and Eaton and Lawrence (35) studied secondary forest in Mexico and found very similar FWD amounts, but still higher CWD amounts, than the values observed in this study (Table 3). Perhaps over time and with continued monitoring, we will see a shift in the distribution of fuels as the larger trees produce more, larger pieces of CWD, and the amount of FWD will decrease.

Another consideration is the timing of these first DWM measurements in relation to the last occurrence of a damaging hurricane in the islands. Hurricanes Georges (1998) and Lenny (1999) were the most recent severe hurricanes to pass over Puerto Rico and the US Virgin Islands, respectively. These hurricanes left in their wake large amounts of DWM and potential forest fuels, as was the case after Hurricane Hugo. Frangi and Lugo (47) estimated that 10% of aboveground biomass in the floodplain forest of the Luquillo Mountains was deposited onto the forest floor by Hurricane Hugo, and Vogt et al. (48) estimated that the hurricane deposited 2.6–9.8 Mg ha^{-1} of woody materials with a diameter >1 cm in the Luquillo Experimental Forest. This study's measurements in Puerto Rico and the US Virgin Islands were taken subsequent to hurricane damage (3–8 y and 5 y, respectively). Five years after the passage of Hurricane Hugo, Vogt et al. (48) observed that fine litterfall had still not recovered to predisturbance levels. Further, based on their observed rates of decomposition and the large amount of material, they postulated that it would require 10 y or more for the woody material deposited by the hurricane to be completely decomposed (48). Vogt et al. (48) expanded on the idea put forth by Lugo and Scatena (45), stating that some forests in Puerto Rico might be in a continuous state of recovery from hurricanes.

However, it is surprising to consider that these islandwide estimates of fuels would be so impacted by the disturbance of Hurricane Georges for so long a time afterward. The damage caused by this hurricane, while widespread and severe, was not consistent across the entire island (49). The long-term effects of hurricanes on fuels cited here occurred entirely within the Luquillo Experimental Forest in the northeastern portion of the island, an area that was heavily impacted by both Hurricane Hugo (1989) and Hurricane Georges (1998). We have to consider that hurricane effects on fuels were more widespread, and that perhaps some other factors are contributing to the increase in FWD and decrease in CWD over time. It seems reasonable that in areas impacted by Hurricane Georges, hurricane-deposited CWD continues to decompose and is almost exhausted and FWD has yet to reach prehurricane levels. However, in areas that were not impacted by the hurricane, perhaps FWD accumulation is related to forest maturation.

CONCLUSIONS

Trends in Caribbean island forest fuel loadings appear to be dynamic and episodic, changing with both natural and anthropogenic disturbance as well as with forest succession. Although total amounts of forest fuels did not change over time, their distribution amongst the size classes is dynamic. One can expect to see periods of high CWD fuel loads subsequent to hurricanes that slowly decrease over the course of several years. Initially, hurricanes will create high FWD fuel loads, but these will decrease quickly and take many years to reach predisturbance levels as stand development slowly progresses. These changes, however, will be additionally affected by an overall increase in downed woody piece size and increased amounts of FWD and forest floor material from normal mortality and leaf fall in maturing forests with increasingly large average tree diameters. Future monitoring will quantify these posthurricane pulses of fuels and subsequent reincorporation into living forest biomass. These pulses of downed fuels drive fuel dynamics and attendant wildfire risks that resource managers and agencies charged with fire protection will have to continually assess and plan for accordingly in tropical island ecosystems such as those found on Puerto Rico.

References and Notes

1. Murphy, P.G. and Lugo, A.E. 1986. Ecology of tropical dry forests. 1986. *Annu. Rev. Ecol. Syst. 17*, 67–88.
2. Weaver, P.L. and Chinea, J.D. 2003. Secondary subtropical dry forest at the La Tinaja tract of the Cartagena Lagoon National Wildlife Refuge, Puerto Rico. 2003. *Carib. J. Sci. 393*, 273–285.
3. Foster, D.R., Fluet, M. and Boose, E.R. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. 1999. *Ecol. Appl. 92*, 555–572.
4. 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*, Dallmeier, F. and Comiskey, J.A. (eds). Parthenon Publishing Group, Washington, DC, pp. 249–270.
5. Weaver, P.L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo mountains. 1989. *Interciencia 144*, 181–192.
6. Weaver, P.L. 1998. The effects of environmental gradients on hurricane impact in Cinnamon Bay watershed, St. John, U.S. Virgin Islands. In: *Forest Biodiversity in North, Central and South American, and the Caribbean*, Dallmeier, F. and Comiskey, J.A. (eds). Parthenon Publishing Group, Washington, DC, pp. 333–348.
7. Reilly, A.E. 1998. Hurricane Hugo: winds of change...or not? Forest dynamics on St. John, U.S. Virgin Islands, 1986–1991. In: *Forest Biodiversity in North, Central and South American, and the Caribbean*, Dallmeier, F. and Comiskey, J.A. (eds). Parthenon Publishing Group, Washington, DC, pp. 349–365.
8. Dallmeier, F., Comiskey, J.A. and Scatena, F.N. 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*, Dallmeier, F. and Comiskey, J.A. (eds). Parthenon Publishing Group, Washington, DC, pp. 231–248.
9. Quiñones, F. 1992. History of hurricanes in Puerto Rico, 1502–1989. 1992. *Acta Cient. 61*, 3–14.
10. Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. 2000. *Nature 403*, 853–858.
11. Parrotta, J.A. 2000. *Leucaena leucocephala* (Lam.) de Wit. Leucaena, tantan. In: *Bioecología de Árboles Nativos y Exóticos de Puerto Rico y las Indias Occidentales*, Francis, J.K. and Lowe, C.A. (eds). USDA Forest Service General Technical Report IITF-115. International Institute of Tropical Forestry, Río Piedras, Puerto Rico, pp. 308–316.
12. Dunphy, B.K., Murphy, P.G. and Lugo, A.E. 2000. The tendency for trees to be multiple-stemmed in tropical and subtropical dry forests: studies of Guánica forest, Puerto Rico. *Trop. Ecol. 412*, 161–167.
13. Van Bloem, S.J., Lugo, A.E. and Murphy, P.G. 2006. Structural response of Caribbean dry forests to hurricane winds: a case study from Guánica forest, Puerto Rico. *J. Biogeogr. 33*, 517–523.
14. Keane, R.E., Burgan, R. and van Wagtendonk, J. 2001. Mapping wildland fuels for fire management across multiple scales: integrating remote sensing, GIS, and biophysical modeling. 2001. *Int. J. Wildland Fire 10*, 301–319.
15. Brandeis, T.J., Helmer, E.H. and Oswalt, S.N. 2007. *The Status of Puerto Rico's Forests, 2003*. USDA Forest Service Southern Research Station, Asheville, North Carolina, 75 pp.
16. Brandeis, T.J. and Oswalt, S.N. 2007. *The Status of U.S. Virgin Islands' Forests, 2004*. USDA Forest Service Southern Research Station, Asheville, North Carolina, 61 pp.
17. Burgan, R.E. 1988. *Revisions to the 1978 National Fire-Danger Rating System*. USDA Forest Service Research Paper SE-273. USDA Forest Service Southeastern Forest Experiment Station, Asheville, North Carolina, 39 pp.
18. Reams, G.A., Smith, W.D., Hansen, M.H., Bechtold, W.A., Roesch, F.A. and Moisen, G.G. 2005. The forest inventory and analysis sampling frame. In: *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures*, Bechtold, W.A. and Patterson, P.L. (eds). USDA Forest Service General Technical Report SRS-80. USDA Forest Service Southern Research Station, Asheville, North Carolina, pp. 11–26.
19. Brandeis, T.J. 2003. Puerto Rico's forest inventory: adapting the forest inventory and analysis program to a Caribbean island. *J. For. 1011*, 8–13.
20. McCollum, J. 2001. Honeycombing the icosahedron and icosahedroning the sphere. In: *Proceedings of the Second Annual Forest and Inventory Symposium*, Reams, G.A., McRoberts, R.E. and Van Deusen, P.C. (eds). USDA Forest Service General Technical Report SRS-47. USDA Forest Service Southern Research Station, Salt Lake City, Utah, pp. 25–31.
21. Ewel, J.J. and Whitmore, J.L. 1973. *The Ecological Life Zones of Puerto Rico and the US Virgin Islands*. USDA Forest Service Institute of Tropical Forestry, Río Piedras, Puerto Rico, 72 pp.
22. Bechtold, W.A. and Scott, C.T. 2005. The forest inventory and analysis plot design. In: *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures*, Bechtold, W.A. and Patterson, P.L. (eds). USDA Forest Service General Technical Report SRS-80. USDA Forest Service Southern Research Station, Asheville, North Carolina, pp. 27–42.
23. USDA Forest Service. 2002. *Field Procedures for Puerto Rico and the Virgin Islands, Supplement C to SRS Regional Manual 1.56*. USDA Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit, Knoxville, Tennessee, 154 pp.
24. Woodall, C. and Williams, M.S. 2005. *Sampling Protocol, Estimation and Analysis Procedures for Down Woody Materials Indicator of the FIA Program*. USDA Forest Service North Central Research Station, St. Paul, Minnesota, 47 pp.
25. Van Wagner, C.E. 1964. The line-intersect method in forest fuel sampling. 1964. *For. Sci. 10*, 267–276.
26. Brown, J.K. 1974. *Handbook for Inventorying Downed Woody Material*. USDA Forest Service Intermountain Forest and Range Experimental Station, Ogden, Utah, 24 pp.
27. Freund, R.J. and Littel, R.C. 1981. *SAS for Linear Models. A Guide to the ANOVA and GLM Procedures*. SAS Series in Statistical Applications. SAS Institute Inc., Cary, North Carolina, 231 pp.

28. Littel, R.C., Henry, P.R. and Ammerman, C.B. 1998. Statistical analysis of repeated measures data using SAS procedures. 1998. *J. Anim. Sci. 76*, 1216–1231.
29. Li, Y., Xu, M., Zou, X., Shi, P. and Zhang, Y. 2005. Comparing soil organic carbon dynamics in plantation and secondary forest in wet tropics in Puerto Rico. 2005. *Global Change Biol. 11*, 239–248.
30. Lugo, A.E., Domínguez Cristóbal, C., Santos, A. and Torres Morales, E. 1999. Nutrient return and accumulation in litter of a secondary forest in the coffee region of Puerto Rico. *Acta Cien. 131*, 43–74.
31. Murphy, P.G. and Lugo, A.E. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica 182*, 89–96.
32. Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A. and Bello-Quintero, N. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *J. Trop. Ecol. 13*, 697–708.
33. Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F. and Veldkamp, E. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *For. Ecol. Manage. 164*, 237–248.
34. Hughes, R.F., Kauffman, J.B. and Jaramillo, V.J. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology 806*, 1892–1907.
35. Eaton, J.M. and Lawrence, D. 2006. Woody debris stocks and fluxes during succession in a dry tropical forest. 2006. *For. Ecol. Manage. 232*, 46–55.
36. Cummings, D.L., Kauffman, J.B., Perry, D. and Hughes, R.F. 2002. Aboveground biomass and structure of rainforests in the southwestern Brazilian Amazon. *For. Ecol. Manage. 163*, 293–307.
37. Nascimento, H.E.M. and Laurance, W.F. 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *For. Ecol. Manage. 168*, 311–321.
38. ter Steege, H. 2001. *Biomass Estimates for Forests in Guyana and Their Use in Carbon Offsets.* International Centre for Rain Forest Conservations and Development, Georgetown, Guyana, 42 pp.
39. Debeljak, M. 2006. Coarse woody debris in virgin and managed forest. 2006. *Ecol. Indic. 6*, 733–742.
40. Chojnacky, D.C. and Schuler, T.M. 2004. Amounts of down woody materials for mixed-oak forests in Kentucky, Virginia, Tennessee, and North Carolina. *South. J. Appl. For. 282*, 113–117.
41. Idol, T.W., Figler, R.A., Pope, P.E. and Ponder, F. Jr. 2001. Characterization of coarse woody debris across a 100 year chronosequence of upland oak-hickory forests. *For. Ecol. Manage. 149*, 153–161.
42. Rubino, D.L. and McCarthy, B.C. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. *For. Ecol. Manage. 183*, 221–238.
43. Birdsey, R.A. 1992. *Carbon Storage and Accumulation in United States Forest Ecosystems.* USDA Forest Service General Technical Report WO-59. USDA Forest Service, Washington, D.C., 51 pp.
44. Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A. and Sevink, J. 2002. High altitude tropical secondary forests: a competitive carbon sink? *For. Ecol. Manage. 163*, 9–25.
45. Lugo, A.E. and Scatena, F.N. 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. In: *Tropical Forests: Management and Ecology*, Lugo, A.E. and Lowe, C. (eds.). Springer-Verlag, New York, pp. 224–257.
46. Oliver, C.D. and Larson, B.C. 1996. *Forest Stand Dynamics* (updated edition). John Wiley and Sons, Inc., New York, 420 pp.
47. Frangi, J.L. and Lugo, A.E. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica 234*, 324–335.
48. Vogt, K.A., Vogt, D.J., Boon, P., Covich, A., Scatena, F.N., Asbjornsen, H., O'Hara, J.L., Pérez, J., Siccama, T.G., Bloomfield, J. and Ranciato, J.F. 1996. Litter dynamics along stream, riparian and upslope areas following Hurricane Hugo, Luquillo Experimental Forest, Puerto Rico. *Biotropica 284*, 458–470.
49. US Geological Survey. 1999. *Puerto Rico.* USGS Fact Sheet 040–99. US Geological Survey, Guaynabo, Puerto Rico, 4 pp.

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RESEARCH ARTICLE

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Coarse Woody Debris in a Southern Appalachian Spruce-fir Forest of the Great Smoky Mountains National Park

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ABSTRACT: Spruce-fir forests in the southern Appalachian Mountains receive high atmospheric nitrogen inputs and have high nitrate levels in soil solution and streamwater. High levels of excess nitrogen have been associated with reduced tree vigor. Additionally, the balsam woolly adelgid (*Adelges piceae* Ratz.) has killed the majority of endemic Fraser fir [*Abies fraseri* (Pursh) Poir.] trees, resulting in large amounts of coarse woody debris. As part of a biogeochemical study in the Great Smoky Mountains National Park, coarse woody debris was sampled to determine volume, mass, change in density, and change in concentration and content of carbon and nitrogen over the decomposition process. Dead wood volume was highly variable across the watershed, ranging from 4.5 m^3 ha^{-1} to 306.8 m^3 ha^{-1} for standing boles and from 21.2 m^3 ha^{-1} to 402.7 m^3 ha^{-1} for down boles. Wood density decreased significantly for all three major overstory species [red spruce (*Picea rubens* Sarg.), yellow birch (*Betula alleghaniensis* Britt.), and Fraser fir] by approximately 60%, from slightly decayed boles to boles in advanced decay. Standing and down dead biomass averaged 39.4 Mg ha^{-1} and 33.8 Mg ha^{-1}, respectively. Carbon concentrations remained relatively constant and were approximately 47% for all decay classes and all species. Nitrogen concentrations increased sharply between live wood and highly decayed wood. The nitrogen content in live wood, compared to wood in advanced decay, increased by 40% to 118% for the species tested. At the watershed level, live bole wood contained 108.4 kg ha^{-1} of nitrogen, and dead bole wood contained 101.5 kg ha^{-1}. Total carbon in live and dead bole wood averaged 93.8 Mg ha^{-1} and 34.9 Mg ha^{-1}, respectively. The magnitude of coarse woody debris in this system is among the highest reported in the literature for the eastern United States, emphasizing the high degree of disturbance that has taken place in this ecosystem.

Index terms: *Abies fraseri, Adelges piceae,* balsam woolly adelgid, biomass, coarse woody debris, disturbance, Fraser fir, mortality, nitrogen saturation, *Picea rubens,* red spruce

INTRODUCTION

The most extensive old-growth southern Appalachian red spruce (*Picea rubens* Sarg.) – Fraser fir [*Abies fraseri* (Pursh) Poir.] forests occur in the Great Smoky Mountains National Park (GRSM) in North Carolina and Tennessee, where approximately 19,666 ha of this vegetation type is found (74% of the total spruce-fir forest in the southern Appalachians) (Dull et al. 1988). Historically, these high-elevation spruce-fir forests have largely escaped logging and fire (Harmon et al. 1983; Pyle and Schafale 1988). Throughout the southern Appalachians, the Fraser fir, which is endemic to the area, has been decimated by a non-native pest, the balsam woolly adelgid (also known as balsam woolly aphid) (*Adelges piceae* Ratz.) (Eagar 1978; Nicholas et al. 1992a). The infestation has resulted in large patches of dead fir trees in areas of pure fir stands and small patches of dead fir where it is co-dominant with spruce. Episodic events or stand replacement disturbances, such as insect infestations and changing environmental conditions, can contribute large amounts of coarse woody debris (CWD) to the forest floor and have a substantial impact on the nutrient cycling in affected areas. Several studies of CWD in spruce-fir forests have been conducted in the Northeastern United States (Lambert et al. 1980; Foster and Lang 1982), the Rocky Mountains (Arthur and Fahey 1990; Laiho and Prescott 1999), and sub-boreal and boreal Canadian forests (Sturtevant et al. 1997; Clark et al. 1998; Hely et al. 2000; Pedlar et al. 2002; Harper et al. 2003). However, few have concentrated on the spruce-fir ecosystem of the southern Appalachians (Nicholas and White 1985).

In addition to elevated levels of mortality, caused by the balsam woolly adelgid, there is evidence that some mature high elevation spruce-fir forests in the southeastern United States may be nitrogen saturated (Lovett 1992; Van Miegroet et al. 1992; Nodvin et al. 1995). These forests receive high levels of atmospheric nitrogen inputs (28 kg ha^{-1} yr^{-1}) and have high nitrate levels in soil solution (10-20 kg ha^{-1} yr^{-1}) and stream water (15 kg ha^{-1} yr^{-1}) (Johnson et al. 1991; Joslin and Wolfe 1992; Nodvin et al. 1995). When nitrogen losses begin to equal or exceed inputs, a system is said to be nitrogen saturated (Ågren and Bosatta 1988; Aber et al. 1989). Impacts to individual trees and stands include decreased foliar calcium, reduced tree growth,

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increased tree mortality rates, and reduced root growth (Joslin and Wolfe 1992; McNulty and Aber 1993; Joslin and Wolfe 1994; Aber et al. 1998; Boggs et al. 2005). These impacts are accomplished primarily through the leaching of cations from foliage and soil and through nitrate-mediated aluminum mobilization, which interferes with cation uptake and causes soil acidification and water quality deterioration (Ågren and Bosatta 1988; Johnson et al. 1991; Joslin et al. 1992; Garten and Van Miegroet 1994; Aber et al. 1998). Several factors predispose forested watersheds to nitrogen saturation, including chronically high rates of nitrogen deposition, advanced stand age, and the presence of large pools of soil nitrogen (Stoddard 1994).

Forest nutrient cycling and nutrient availability, especially in areas experiencing multiple stressors, cannot be fully understood without considering the CWD component, as it accounts for a significant store of biomass and nutrients within an ecosystem (Harmon et al. 1987; Keenan et al. 1993). CWD may also be a sink for nutrients, especially nitrogen, during portions of the decay process (Grier 1978; Edmonds and Marra 1999). As wood decays, the carbon to nitrogen (C/N) ratio decreases; respiration and leaching cause the proportion of carbon to decrease, while nitrogen immobilization during initial stages of decay causes the proportion of nitrogen to increase (Schlesinger 1991). This increase in nitrogen is of particular importance in areas of high nitrogen deposition and high amounts of CWD, because the dead wood may be a temporary sink for nitrogen and have an effect on nitrogen saturation. Assessing the role of CWD as a sink for nitrogen is complicated by the fact that changes in nitrogen concentration are affected by changes in wood density as the wood decays, both of which tend to be species and ecosystem specific. Determination of this potential is also confounded by the heterogeneity of CWD within a stand.

A nutrient cycling study was initiated in 1991 in a 17.4 ha spruce-fir forest watershed in the Great Smoky Mountains National Park. Species composition, stand structure, streamwater and soil water chemistry, as well as nitrogen and sulfur deposition have been monitored to understand the different components of nutrient cycling within a nitrogen saturated watershed (Johnson et al. 1991; Johnson et al. 1992; Nodvin et al. 1995; Shubzda et al. 1995; Pauley et al. 1996). Information regarding the dynamics and distribution of CWD from a study of this scale lends insight into how it interacts with other watershed issues. The objectives of this study were to determine: (l) the magnitude and spatial variability in CWD across a small watershed; (2) the wood density at different stages of decay for the three major overstory species [red spruce, yellow birch (*Betula alleghaniensis* Britt.), and Fraser fir]; and (3) the concentration and density-adjusted content of carbon and nitrogen of dead wood in order to estimate nutrient storage in the CWD component of a southern Appalachian spruce-fir ecosystem.

METHODS

Study Area

The spruce-fir forests of the GRSM range in elevation from 1500 m to 2000 m (Nicholas 1992). The area receives an average of 210 cm precipitation per year. Temperatures range from –11 °C to 8 °C in the winter and from 12 °C to 25 °C in the summer (1979-1990 data courtesy of GRSM).

The 17.4 ha Noland Divide Watershed (NDW) (35°34'N 83°29'W) is located on the upper reach of Noland Creek in the GRSM (Figure 1). The elevation of NDW ranges from 1676 m to 1921 m. Overstory vegetation is dominated by red spruce, yellow birch, and Fraser fir, which account for 64%, 14%, and 19% of the basal area, respectively. Typical mid-story species include mountain maple (*Acer spicatum* Lam.), mountain ash (*Sorbus americana* Marsh.), pin cherry (*Prunus pensylvanica* L. f.), and downy serviceberry [*Amelanchier arborea* (Michx. f.) Fern.] (Pauley et al. 1996). Basal area averages 39.6 m^2 ha^{-1} for live trees and 19.6 m^2 ha^{-1} for standing dead trees (Pauley et al. 1996). In 2000, the average age of overstory trees was 184 years. The oldest spruce was just over 400 years old, and the oldest fir was 90 years old (Creed et al. 2004b). Soils in the spruce-fir zone tend to be highly acidic with relatively low base saturation (Fernandez 1992). In the watershed, the soils are Inceptisols classified as Dystrochrepts or Haplumbrepts (Johnson et al. 1991; Van Miegroet et al. 1993). They have a silt loam to sandy loam texture and are generally shallow throughout the watershed (< 50 cm depth to bedrock) (Van Miegroet et al. 2001).

Field and laboratory techniques

In 1993, fifty 20-m x 20-m plots (0.04 ha) were established systematically along nine elevation bands ranging from 1700 m to 1911 m in the NDW (Figure 1). All live and standing dead trees ≥ 5.0 cm diameter at breast height (dbh) were measured. Pauley et al. (1996) describes live species composition and stand structure within NDW.

In 1994, down CWD was mapped and identified by species in each of the 50 plots within at least two randomly chosen 10-m x 10-m subplots. Length, diameter at each end, and diameter at the midpoint, were recorded for all down boles. Down CWD was defined as woody material ≥ 10 cm in diameter at the large end and ≥ 1.54 m in length (Nicholas 1994). This is roughly comparable to the 7.6 cm diameter, 100-hour-plus size class used by Nicholas and White (1985). Decay classes were defined as follows: (1) class I: slightly decayed (penetration of a 0.5 cm diameter metal rod into the wood < 0.5 cm); (2) class II: moderately decayed (penetration to the center of the bole); and (3) class III: advanced decay (penetration through the bole). Decay classification follows methods used by Lambert et al. (1980), Bingham and Sawyer (1988), and Clark et al. (1998). Percentage of bark coverage, heartwood and sapwood sponginess, and presence of leaves and twigs were also determined (Nicholas 1994). Total height was measured on all standing dead trees. Species not identifiable in the field were sampled and identified in the laboratory. Time and cause of death of standing and down dead trees were not determined.

Wood samples were taken from the three major overstory species (red spruce, Fraser

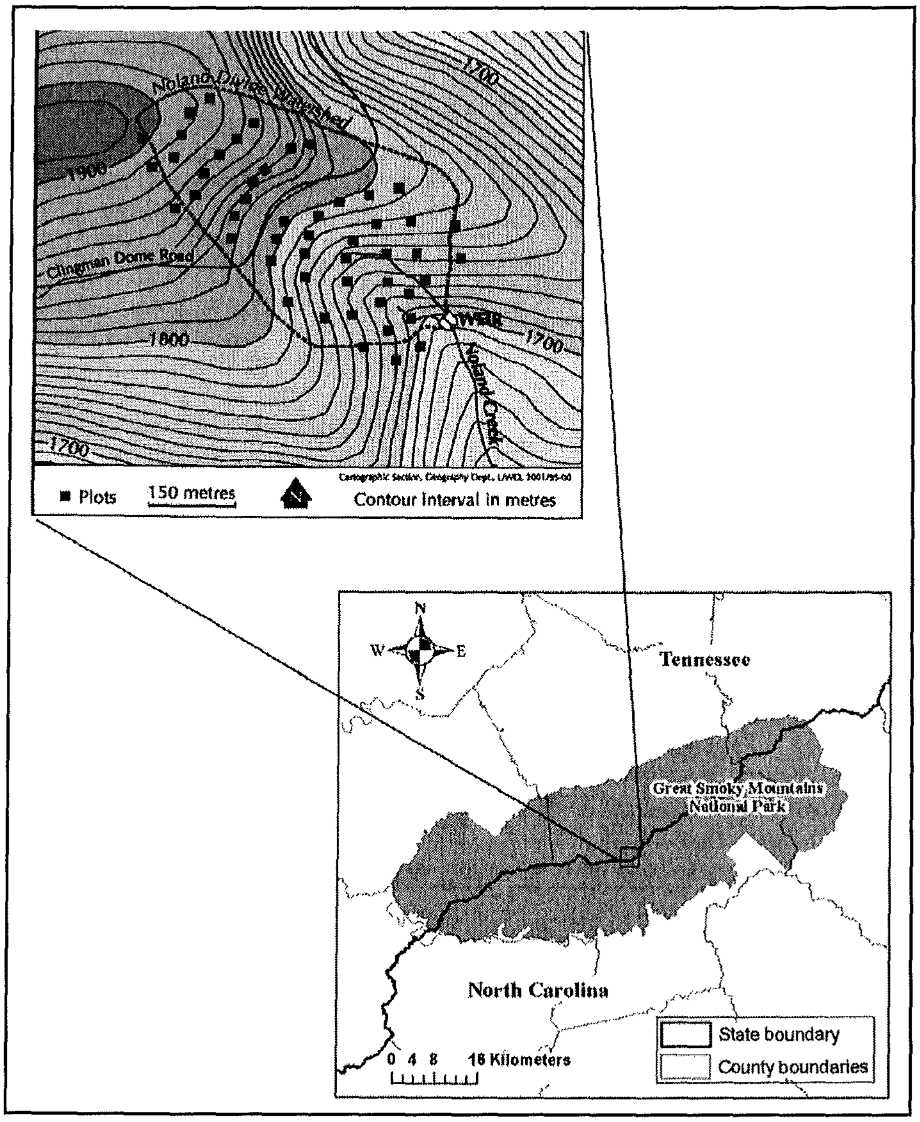

Figure 1. The Great Smoky Mountains National Park and location of Noland Divide Watershed study site.

fir, and yellow birch). Bark was not included in the study, because it constitutes a minor fraction of the dry mass of most boles. In addition, Fraser fir tends to lose bark very soon after death (only about 20% of down boles had bark). Cross-sections were taken from down CWD. Increment cores were taken from live trees of each species. For standing dead boles, either a wedge was taken without felling the tree or a cylinder of wood of known volume was removed using a brace and 1.9 cm diameter drill bit. An earlier evaluation of the data indicated that the brace and bit method and the wedge method were not significantly different for sound boles (J. Shen, unpubl. data). All samples were wrapped in aluminum foil and placed in plastic bags for transportation.

Samples for nutrient analysis were weighed, dried at 70 °C to constant weight, and ground in a Wiley mill to pass through a fine mesh screen. Nitrogen and carbon concentrations were determined with a Leco CNS 2000 apparatus (Leco Corp., St. Joseph, MI) (carbon via an infrared cell, and nitrogen via a thermal conductivity cell). Due to the variability in decay class II boles and the higher level of subjectivity involved when assigning this decay rating, only live trees and decay class I and III boles were tested for nutrient concentrations.

Wood density samples were weighed and volume determined by water displacement. Samples were then dried at 70 °C to constant weight. Wood density was obtained by dividing the dry weight of a sample by its fresh displacement volume.

Data analysis

Volume of logs was calculated using the formula for a frustum of a cone (the part of the cone that is left when the top is removed parallel to the base),

$$Volume = (L/3)*(A_l + \mathrm{sqrt}(A_l)(A_s) + A_s)$$

(Husch et al. 1972)

where L is the length of the log, A_l and A_s are cross-sectional areas of the log at the point where the large and small diameters were measured. The volume of standing dead trees was calculated as the volume of a paraboloid (a slightly convex or rounded cone),

$$Volume = ½*A_b*Ht$$

(Husch et al. 1972)

where A_b is the cross sectional area of the base calculated using diameter taken at breast height, and Ht is the height of the tree. Biomass of dead wood was calculated by multiplying the bole volume by the mean wood density for the appropriate species and decay class. The magnitude of carbon and nitrogen pools contained in standing and down wood was estimated by multiplying the biomass of the wood by the appropriate mean nutrient concentration. Nitrogen and carbon concentrations for decay class II boles were estimated by species based on live and decay class I and III data using the general linear model (GLM) procedure in SAS (SAS Institute 1990). Resulting decay class II nutrient values were found to be comparable to published values (Arthur and Fahey 1990; Creed at al. 2004a).

Main effects of independent variables were examined with separate analysis of variance (ANOVA) tests using the GLM procedure in SAS. For reporting purposes, three elevation classes were defined as 1700-1756 m (low) (n = 19 plots), 1783-1834 m (medium) (n = 19 plots), and 1865-1911 m (high) (n = 12 plots). Tukey's multiple range test was used to determine if differences existed for dependent variables among species and decay classes. Variables judged to be non-normal (at the 0.01 level), via a Shapiro-Wilks test, were square root transformed for comparisons between classifications and to test for significant independent variables. All tests were considered significant at the 0.05 alpha level.

RESULTS

Stand structure and CWD characterization

Within the NDW, 42% of all standing trees (≥ 5.0 cm dbh) were dead. For the three major overstory species, 70% of standing Fraser fir trees were dead, while only 16% of standing red spruce and 11% of standing yellow birch were dead. Collectively, 15% percent of the other species (mountain maple, mountain ash, pin cherry, and downy serviceberry) were dead.

Stem density of live trees in the NDW averaged 761 stems ha^{-1}, while standing and down CWD averaged 559.5 stems ha^{-1} and 692.1 boles ha^{-1}, respectively (Table 1). Fraser fir accounted for 82% of all standing dead trees and 61% of all down dead boles. For Fraser fir, standing dead trees (max dbh = 60.9 cm) tended to be larger than live trees (max dbh = 34.5 cm), with down dead boles being the largest (max dbh = 82.0 cm) (Figure 2). Red spruce however, had a more even diameter distribution. Diameter distributions of down Fraser fir boles also varied between decay classes. The average diameter for decay class I Fraser fir boles was 18.2 cm (8.8 S.D.), while average diameters for decay class II and III down boles were successively larger, 21.8 cm (10.7 S.D.), 26.7 cm (15.8 S.D.), respectively. There were significantly more decay class I and II Fraser fir boles ha^{-1} than yellow birch and red spruce ($p < 0.0001$) (Figure 3). Additionally, there were significantly more decay class II boles than decay class I and III for both red spruce and Fraser fir ($p < 0.0001$) (Figure 3).

Basal area of live trees averaged 39.6 m^2 ha^{-1} (Table 1). Red spruce accounted for 77% of the live basal area, while yellow birch, Fraser fir, and other species accounted for 18.6%, 2.6%, and 1.7%, respectively. Basal area of standing dead averaged 18.5 m^2 ha^{-1}. In contrast to the live basal area, Fraser fir accounted for 55.1% of standing dead and red spruce 37.8%. Yellow birch accounted for only 5.4% of the standing dead basal area.

Volume

Volume of live trees, standing dead CWD, and down dead CWD was highly variable between plots. Live volume ranged from 145.6 m^3 ha^{-1} to 839.5 m^3 ha^{-1} and averaged 460.6 m^3 ha^{-1} (Table 1). Standing dead volume ranged from 4.5 m^3 ha^{-1} to 306.8 m^3 ha^{-1} (average = 116.7 m^3 ha^{-1}), and down dead volume ranged from 21.2 m^3 ha^{-1} to 402.7 m^3 ha^{-1} (average = 158.8 m^3 ha^{-1}) (Table 1). Red spruce and Fraser fir each accounted for just over 45% of standing and down dead volume in the NDW. Although volume of down CWD tended to decrease with an increase in elevation, and that of standing dead increased, the total volume of CWD was nearly equal for each elevation class (Figure 4). These differences were not significant. Volume of live, standing dead, and down dead Fraser fir, as well as volume of live yellow birch, varied significantly with elevation. In general, live Fraser fir increased from 1.0 m^3 ha^{-1} at elevations < 1865 m to 11.8 m^3 ha^{-1} at elevations ≥ 1865 m. In contrast, live yellow birch volume decreased from 115.0 m^3 ha^{-1} at elevations < 1783 m to 7.7 m^3 ha^{-1} at elevations ≥ 1865 m. Volume of standing dead fir averaged 37.4 m^3 ha^{-1} at low, 62.2 m^3 ha^{-1} at medium, and 83.1 m^3 ha^{-1} at high elevations. Down dead fir averaged 97.5 m^3 ha^{-1} at low, 67.4 m^3 ha^{-1} at medium, and 46.8 m^3 ha^{-1} at high elevations.

Wood density and biomass

To estimate mass of CWD in the NDW, we first determined the wood density of the three principle species by decay class. Density decreased by approximately 60% from decay class I to decay class III and was highly variable within classes (Table 2). An ANOVA on square-root transformed wood density values indicated a highly significant species ($p = 0.0004$) and decay class ($p = 0.0001$) effect for standing and down boles (Table 3). For both Fraser fir and red spruce, density averaged approximately 0.34 g cm^{-3} for standing dead decay class I, and decreased to 0.13 g cm^{-3} for down dead decay class III. Density of yellow birch averaged 0.45 g cm^{-3} in standing dead decay class I and 0.18 g cm^{-3} in down dead decay class III.

Live biomass averaged 201.5 Mg ha^{-1}, and ranged from 62.2 Mg ha^{-1} to 353.5 Mg ha^{-1} (Table 1). Down CWD biomass for all species averaged 33.8 Mg ha^{-1} (min = 4.9 Mg ha^{-1}, max = 89.9 Mg ha^{-1}). Standing dead contributed an additional 39.4 Mg ha^{-1} (min = 1.5 Mg ha^{-1}, max = 102.0 Mg ha^{-1}) for a total of 73.2 Mg ha^{-1} of dead biomass (min = 20.9 Mg ha^{-1}, max = 124.2 Mg ha^{-1}), and 274.7 Mg ha^{-1} of total biomass (min = 158.5 Mg ha^{-1}, max = 441.5 Mg ha^{-1}) (Table 1).

Carbon and Nitrogen

To estimate watershed-level nutrients in CWD, we first determined carbon and nitrogen concentrations for the three principle species by decay class. The carbon concentration averaged 47% for all three species in live wood, and increased slightly, although significantly, to 49% in decay class III wood (Table 2). An analysis of variance also showed a significant species effect (Table 3). For all conditions of wood tested except down decay class III, the percentage of carbon in Fraser fir was significantly higher than the percentage of carbon in yellow birch. Decay class II boles were estimated as having an average of 47% carbon. Density-adjusted carbon content decreased significantly from 169 kg m^{-3} in live wood to 65 kg m^{-3} in down decay class III wood for Fraser fir, a 61%

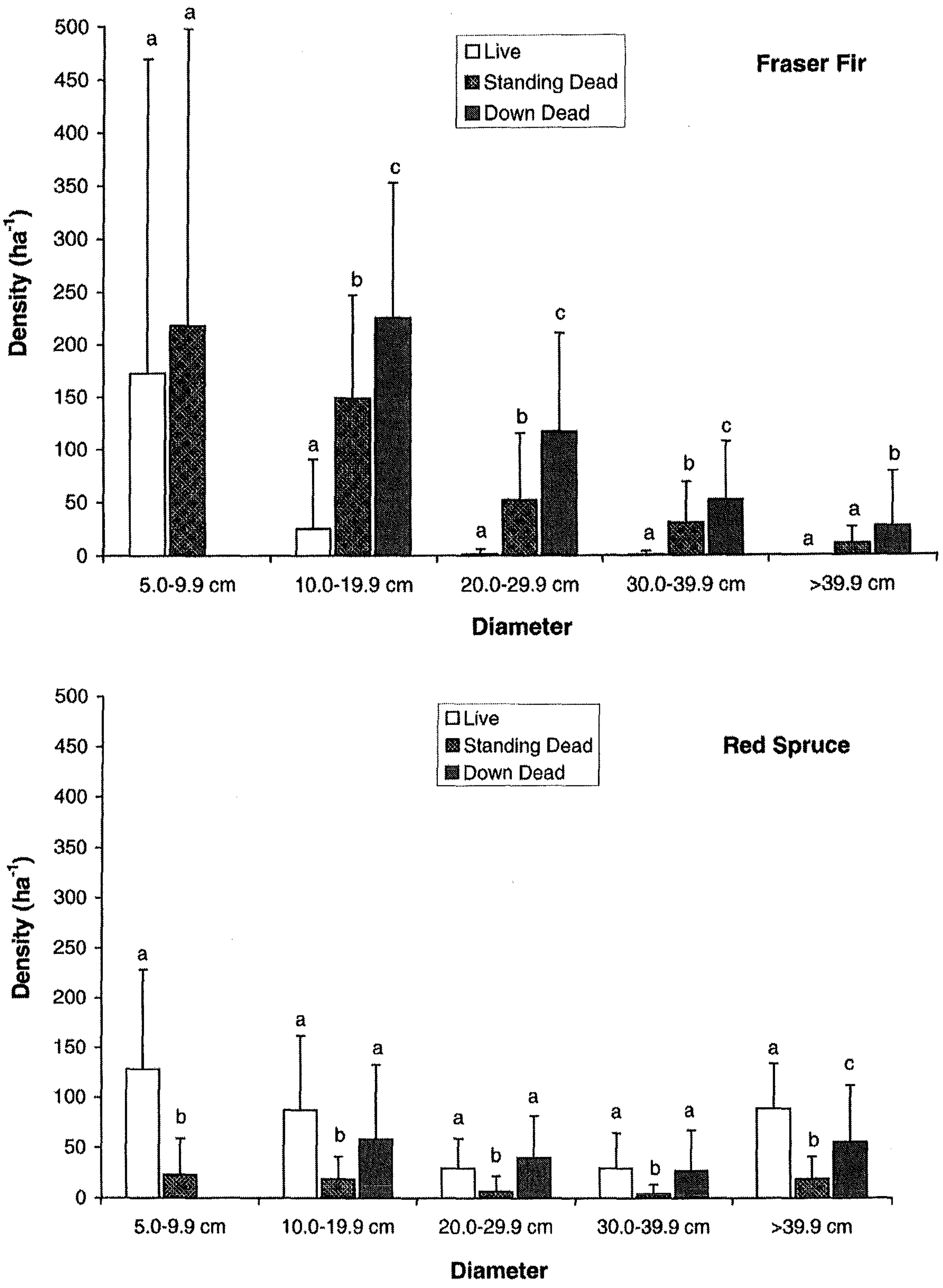

Figure 2. Density by diameter class for Fraser fir and red spruce NDW, GRSM, 1994 (n = 50 plots). Live and standing dead includes trees ≥ 5.0 cm dbh. Down dead includes boles ≥ 10.0 cm diameter at the large end. Sample statistics are the mean and standard deviation. Bar values within the same species and diameter class with the same letter are not significantly different (α = 0.05) based on Tukey's studentized range test.

Table 1. Stem density, basal area, volume, and biomass by species in the NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and the standard deviation in parentheses.

		Live[a]	Standing Dead[a]	Down Dead[b]
Stem Density			stems ha^{-1}	
	Fraser Fir	199.0 (354.1)	460.0 (363.8)	422.4 (184.0)
	Red Spruce	362.5 (156.9)	71.5 (54.9)	180.8 (129.6)
	Yellow Birch	135.0 (147.2)	16.5 (26.5)	52.8 (73.4)
	Other[c]	64.5 (79.1)	11.5 (20.3)	36.0 (63.5)
All species		761.0 (350.3)	559.5 (389.2)	692.1 (204.4)
Basal Area			m^2 ha^{-1}	
	Fraser fir	1.0 (2.0)	10.2 (6.3)	–
	Red Spruce	30.6 (13.1)	7.0 (7.5)	–
	Yellow Birch	7.4 (9.4)	1.0 (2.2)	–
	Other	0.7 (1.0)	0.3 (1.0)	–
All species		39.6 (11.8)	18.5 (10.5)	–
Volume			m^3 ha^{-1}	
	Fraser Fir	3.5 (7.6)	57.8 (41.8)	73.9 (61.0)
	Red Spruce	385.4 (184.0)	53.7 (70.5)	72.8 (66.7)
	Yellow Birch	67.6 (91.2)	4.5 (12.5)	8.8 (16.8)
	Other	4.2 (6.7)	0.7 (2.3)	3.4 (6.7)
All species		460.6 (166.0)	116.7 (82.0)	158.8 (94.0)
Biomass			Mg ha^{-1}	
	Fraser Fir	1.3 (2.8)	18.2 (13.5)	15.9 (12.5)
	Red Spruce	165.7 (79.1)	19.1 (24.6)	14.8 (13.6)
	Yellow Birch	34.5 (46.6)	2.1 (5.7)	3.1 (6.0)
All species		201.5 (72.4)	39.4 (28.0)	33.8 (20.4)

[a] Stems ≥ 5.0 cm dbh

[b] Boles ≥ 10.0 cm in diameter at large end

[c] Other includes: mountain maple, mountain ash, pin cherry, and downy serviceberry

– = no value for cell

change. Carbon content in red spruce and yellow birch also decreased significantly from live wood to down decay class III wood (200 kg m^{-3} to 70 kg m^{-3} for red spruce and 236 kg m^{-3} to 104 kg m^{-3} for yellow birch) (Table 2).

Significant increases in nitrogen concentration between live and decay class III were recorded for all species (Table 2). Nitrogen concentrations increased an average of 304% for Fraser fir, 502% for red spruce, and 483% for yellow birch. There was a significant effect of species, decay class, and the interaction of species and decay class on percent nitrogen (Table 3). For red spruce and Fraser fir combined, wood density explained approximately 50% of the variation in percent nitrogen ($p < 0.0001$) (Figure 5). All three species were significantly different from each other for live wood (Table 2). In decay class III wood, Fraser fir and red spruce did not differ significantly, but both were different from yellow birch. Nitrogen concentrations were always highest in yellow birch, followed by Fraser fir and red spruce. Density-adjusted nitrogen content increased, although not significantly, from 268.6 g m^{-3} in live wood to 380.3 g m^{-3} in down decay class III wood for Fraser fir, a 41% change. For red spruce, nitrogen content increased significantly from 187.8 g m^{-3} to 353.5 g m^{-3}, an 88% change. For yellow birch, nitrogen increased significantly from 512.2 g m^{-3} to 1118.7 g m^{-3}, a 118% change (Table 2).

The C/N ratio showed a steady decline over decay class. Initial C/N ratios for live wood were highest in red spruce (1113), followed by Fraser fir (654), and yellow birch (467) (Table 2). Ratios for decay class III samples averaged 245 for red spruce, 259 for Fraser fir, and 101 for yellow birch. An analysis of variance on square root transformed C/N ratios showed significant effects of species ($p = 0.0001$), decay class ($p = 0.0001$), and the interaction of species and decay class ($p= 0.0001$).

The estimates for wood density, nitrogen content, and carbon content were used to calculate total nitrogen and carbon in bole wood at the watershed level. Live bole wood within the NDW contained an estimated 108.4 kg ha^{-1} of nitrogen, with 67% of this in the red spruce component (Table 4). Dead wood contained another 101.5 kg ha^{-1} of nitrogen, or 48% of the total (209.9 kg ha^{-1}). Standing and down CWD each constituted about one-half of the 101.5 kg ha^{-1} of nitrogen. When total nitrogen in foliage (182 kg ha^{-1}), bark (106.8 kg ha^{-1}), and branch wood (90.8 kg ha^{-1}) was included (Barker et al. 2002), CWD accounted for 17% of the total (589.8 kg ha^{-1}) (Table 5). Fraser fir accounted for 8.7%, red spruce 6.9%, and yellow birch 1.6% of the total.

DISCUSSION

The percentage of standing trees that were dead in NDW (42%) was within the range

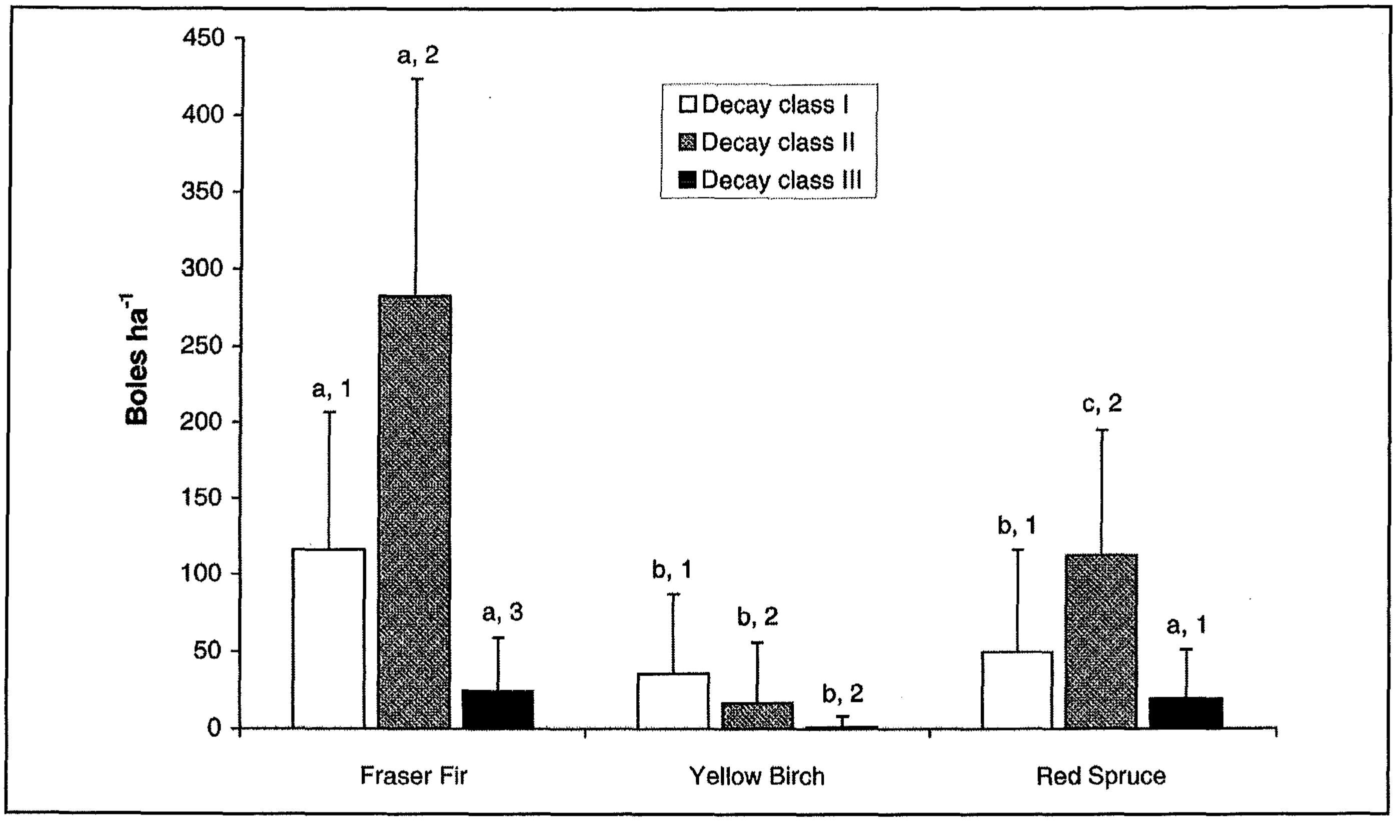

Figure 3. Stem density of down CWD by species and decay class NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and standard deviation. Bar values within the same decay class with the same letter are not significantly different; bar values within the same species with the same number are not significantly different (α = 0.05) based on Tukey's studentized range test.

reported for spruce-fir stands from the Black Mountains in North Carolina, where between 19% and 54% of all stems were dead (Nicholas et al. 1992a). The percentage dead in NDW exceeded the range of 5% to 36% of standing dead trees for a second growth northern hardwood stand in the Northeast (Tritton and Siccama 1990). This underscores the high degree of disturbance that has taken place in this ecosystem. Basal area for live (14.9 to 67.5 m^2 ha^{-1}) and standing dead (1.2 to 42.9 m^2 ha^{-1}) for the current study was slightly more variable than basal area for live (23.8 m^2 ha^{-1} to 46.8 m^2 ha^{-1}) and standing dead trees (9.2 m^2 ha^{-1} to 29.2 m^2 ha^{-1}) in other southern Appalachian spruce-fir forests (Nicholas et al. 1992a).

The uneven diameter distribution observed for Fraser fir in this study is due to the adelgid infestation that has killed the majority of large mature Fraser fir trees. Small fir trees typically have smooth bark and are somewhat more resistant to the adelgid than larger more mature trees, which have developed fissured bark (Eagar 1984). Historically, Fraser fir trees typically attained diameters of at least 50 cm (Eagar 1978).

Volume of down CWD in this study (158.8 m^3 ha^{-1}) was comparable to CWD in other mid and high elevation spruce-fir stands that were infested by the adelgid 3 to 17 years prior to measurement (146.9 m^3 ha^{-1} to 186.0 m^3 ha^{-1}) (Nicholas and White 1985). Down CWD in this study was also somewhat comparable to that reported from other old growth stands in the GRSM (134.3 m^3 ha^{-1}) (Webster and Jenkins 2005). However, snag density reported by Webster and Jenkins (2005) (56.4 stems ha^{-1} to 126.8 stems ha^{-1}) was substantially lower than that for this study (560 stems ha^{-1}). The differences could be attributed in part to their sampling only standing dead trees that were ≥ 10.0 cm dbh, while the present study had a minimum of 5.0 cm dbh. Primarily, however, the differences are most likely due to the high number of dead trees killed by the adelgid.

Decreasing wood density with increasing decay class has been noted by other researchers (Erickson et al. 1985; Arthur and Fahey 1990; Alban and Pastor 1993; Busse 1994). In addition, the wood density values obtained in this study are comparable to those in other spruce-fir studies. In the White Mountains of New Hampshire, red spruce wood density dropped from 0.43 g cm^{-3} in fresh boles to 0.13 g cm^{-3} in highly decayed boles (Foster and Lang 1982). In that same study, balsam fir [*Abies balsamea* (L.) Mill.] wood density dropped from 0.33 g cm^{-3} in fresh boles to 0.19 g cm^{-3} in highly decayed boles. For both red spruce and Fraser fir, in the current study, wood density dropped from 0.34 g cm^{-3} in decay class I wood to 0.13 g cm^{-3} in decay class III wood. Wood density in boles from a Rocky Mountain Engelmann spruce – subalpine fir [*Picea engelmannii* Parry – *Abies lasiocarpa* (Hook.) Nutt.]

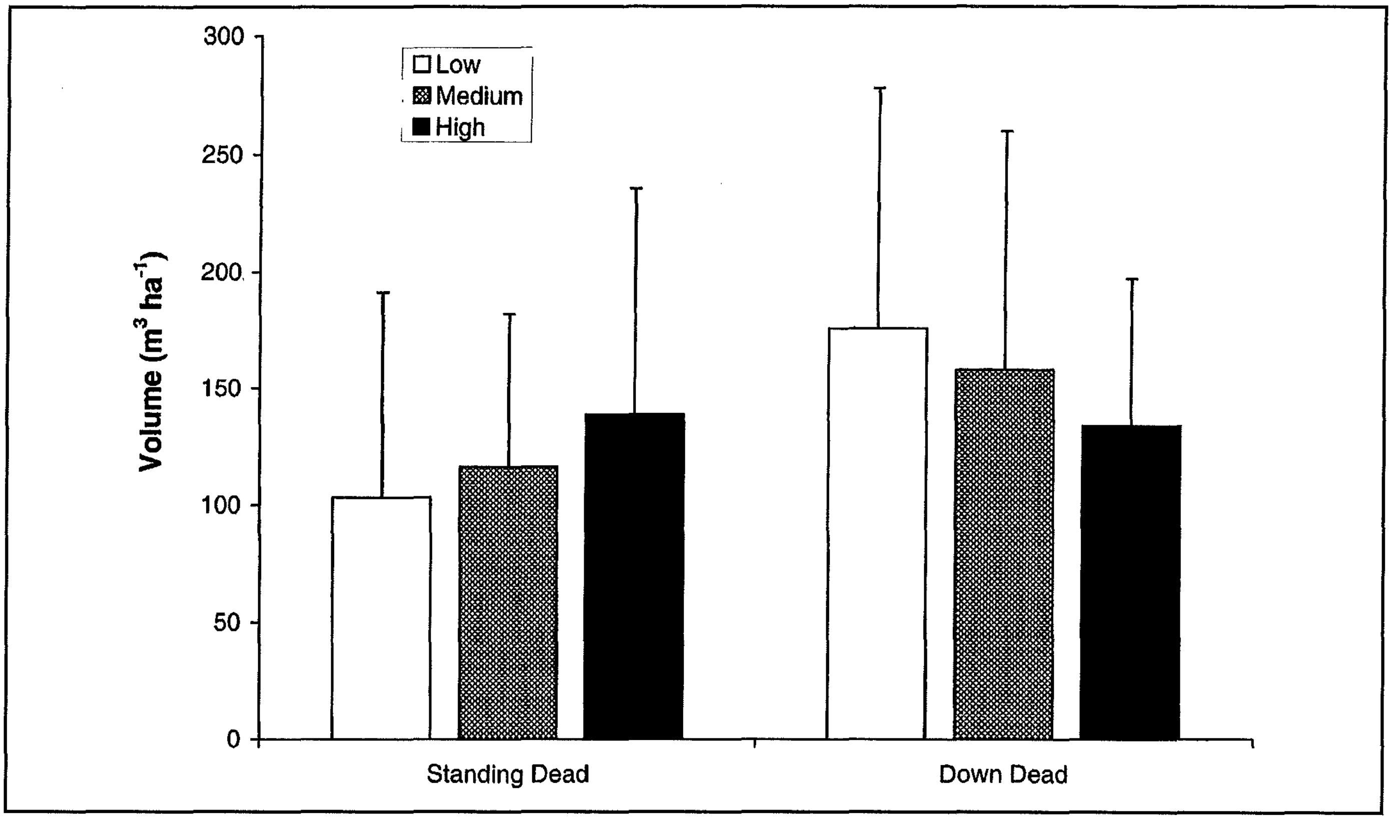

Figure 4. Volume of CWD by elevation class (no significant differences) (low = 1700-1756 m (n = 19 plots); medium = 1783-1834 m (n = 19 plots); high = 1865-1911 m (n = 12 plots)) NDW, GRSM, 1994. Sample statistics are the mean and standard deviation.

forest decreased from 0.31 g cm^{-3} (decay class I) to 0.17 g cm^{-3} (decay class V) (Arthur and Fahey 1990).

Biomass of CWD typically ranges from 10 to 511 Mg ha^{-1} for various temperate forested ecosystems and accounts for 1.3% to 45.1% of the total aboveground biomass (Harmon et al. 1986). CWD in the NDW accounted for 27% of the total biomass (not including woody species < 5.0 cm dbh or fine woody debris) and ranged from 20.9 Mg ha^{-1} to 124.2 Mg ha^{-1}. The percentage of total biomass that was dead was highly variable by species. Ninety-six percent of the total biomass of Fraser fir was in the CWD component. In contrast, 17% of total red spruce biomass was CWD.

Results from our nitrogen analyses indicate that nitrogen concentration increases with decay, as does nitrogen content, although to a lesser degree. This phenomenon has been documented by others and may be indicative of external nitrogen sources, such as throughfall, nitrogen fixation, and litter fall (Foster and Lang 1982; Sollins et al. 1987; Arthur and Fahey 1990; Alban and Pastor 1993; Busse 1994; Brown et al. 1996; Krankina et al. 1999).

The C/N ratios for Fraser fir (live = 654, decay class III = 259) were very similar to those reported for balsam fir in New Hampshire (live = 714, down dead = 208) (Foster and Lang 1982). Given that our C/N ratio for red spruce decay class III (245) was higher than that reported by Foster and Lang (1982) for the same species (71), our decay class III samples may not reflect the most highly decayed wood in the watershed. Additionally, the relatively high C/N ratios of decay class III wood, as compared to soil (typically 8 to 15), may be indicative of net nitrogen immobilization (McNulty and Aber 1993; Brady and Weil 1996).

In this study, CWD accounted for 101.5 kg ha^{-1} of nitrogen, which was 17% of the total (589.8 kg ha^{-1}). This was comparable to a spruce-fir forest in Colorado, where CWD accounted for 91 kg ha^{-1} of nitrogen, which was 18% of the total (507 kg ha^{-1}). However, when forest floor and belowground nitrogen was taken into consideration, CWD only accounted for 7% of the total (1,355 kg ha^{-1}) (Arthur and Fahey 1990).

Within the NDW, total carbon in live and dead bole wood averaged 128.7 Mg ha^{-1}, of which 34.9 Mg ha^{-1} was the dead portion. In contrast to watershed nitrogen, where CWD made up 48% of the total contained in bole wood, CWD only constituted 27% of the total carbon. This percentage would undoubtedly be lower if foliage, bark, and branch wood were included in the total estimate. In a balsam fir forest, the majority of carbon was in the soil and forest floor, and down CWD only accounted for 3% of the total carbon contained in various detrital components (Lang et al. 1981).

Table 2. Summary of wood density, nitrogen, carbon, and C/N ratios for live, standing dead, and down dead trees by species and decay class in the NDW, GRSM, 1994. Sample statistics are the mean and the standard deviation in parentheses.

Species	Condition	Decay Class	n	Density (g cm^{-3})	n[b]	%N	N (g m^{-3})	%C	C (kg m^{-3})	C/N
Fraser Fir	Live	–	–	0.36[a]	17	0.075a (0.02)	269a (55)	47.0a (1.5)	169a (5)	654a (132)
	Standing Dead	1	27	0.337a (0.09)	27	0.116a (0.06)	390a (187)	48.2a,b (1.7)	162a (6)	493a (185)
		2	25	0.296a (0.08)	–	0.166[c]	–	47.9[c]	–	
	Down Dead	1	14	0.293a (0.07)	33	0.108a (0.06)	317a (167)	47.6a,b (1.5)	141b (18)	553a (245)
		2	28	0.208b (0.07)	–	0.166[c]	–	47.9[c]	–	
		3	15	0.130c (0.04)	13	0.303b (0.21)	380a (223)	48.6b (2.5)	65c (17)	259b (176)
Red Spruce	Live	–	–	0.43[a]	29	0.044a (0.008)	188a (34)	46.6a (0.6)	200a (3)	1113a (274)
	Standing Dead	1	12	0.336a (0.12)	27	0.083a,b (0.03)	262a,b (82)	47.6a,b (2.3)	153b (30)	629b (184)
		2	7	0.383a (0.05)	–	0.135[c]	–	47.7[c]	–	
	Down Dead	1	5	0.314a,b (0.10)	16	0.111b (0.08)	355b (254)	47.4a,b (1.3)	155b (20)	579b (271)
		2	13	0.193b,c (0.05)	–	0.135[c]	–	47.7[c]	–	
		3	7	0.126c (0.02)	10	0.265c (0.14)	353b (165)	49.0b (3.2)	70c (23)	245c (146)
Yellow Birch	Live	–	7	0.511a (0.05)	23	0.100a (0.01)	512a (64)	46.2a (0.87)	236a (4)	467a (55)
	Standing Dead	1	10	0.452a (0.15)	18	0.136a (0.06)	576a (219)	46.3a (2.0)	205b (48)	396a (143)
		2	7	0.481a (0.11)	–	0.274[c]	–	47.2[c]	–	
	Down Dead	1	17	0.388a,b (0.10)	20	0.160a (0.10)	586a (348)	46.6a (1.4)	175b (36)	362b (136)
		2	13	0.293b,c (0.10)	–	0.274[c]	–	47.2[c]	–	
		3	5	0.181c (0.13)	6	0.583b (0.25)	1118b (414)	49.3b (2.0)	104c (46)	101c (49)

NOTE: Values within the same species followed by the same letter are not significantly different ($\alpha = 0.05$) based on Tukey's studentized range test for contrasts among means.

[a] Values are taken from Foster and Lang (1982) for balsam fir and red spruce.

[b] Values for this n apply to %N, N (g m^{-3}), %C, C (kg m^{-3}) and C/N.

[c] Values estimated via the GLM procedure in SAS.

– = no value for cell

Table 3. Analysis of variance for the main effects of species (Fraser fir, red spruce, yellow birch), decay class for density (standing dead – I, II; down dead – I, II, III), for percent nitrogen, and percent carbon (live, standing dead – I, down dead – I, III), and the interaction of species and decay class, in the NDW, GRSM, 1994 (n = 50 plots).

	Density (g cm^{-3})[a]			Nitrogen (%)[a]			Carbon (%)		
Source	df	F value	Pr > F	df	F value	Pr > F	df	F value	Pr > F
Species	2	8.3	0.0004	2	8.5	0.0005	2	4.5	0.012
Decay Class	4	19.8	0.0001	3	47	0.0001	3	8.1	0.0001
Species * Decay Class	8	1.3	0.2586	6	3.6	0.0023	6	2	0.072

[a] Square-root transformed

CONCLUSIONS

Values for wood density, nitrogen concentration and content, as well as C/N ratios, were highly variable within decay classes, pointing to possible limitations of the use of decay class as a predictor of stage of decay. Daniels et al. (1997) found that decay class had a weak relationship with time since tree death for *Thuja plicata* (Donn ex D. Don *in* Lamb.) in a hemlock forest of southwestern coastal British Columbia, indicating that using time since death, rather than decay class, may better predict nutrient concentrations and content within decaying wood. Creed et al. (2004b) also found this to be true for wood density of red spruce and Fraser fir. However, none of the techniques tested could explain more than 53% of the variation in wood density. In contrast, Naesset (1999) found that decay class correlated well with wood density. That we found wood density to explain approximately 50% of the variation in percent nitrogen suggests that a more accurate measurement of wood density might better predict decay stage and, therefore, percent nitrogen, than decay class. Ultimately, this would mean better estimates of nitrogen at the watershed level.

Besides an increase in the amount of CWD, impacts to this ecosystem from the balsam

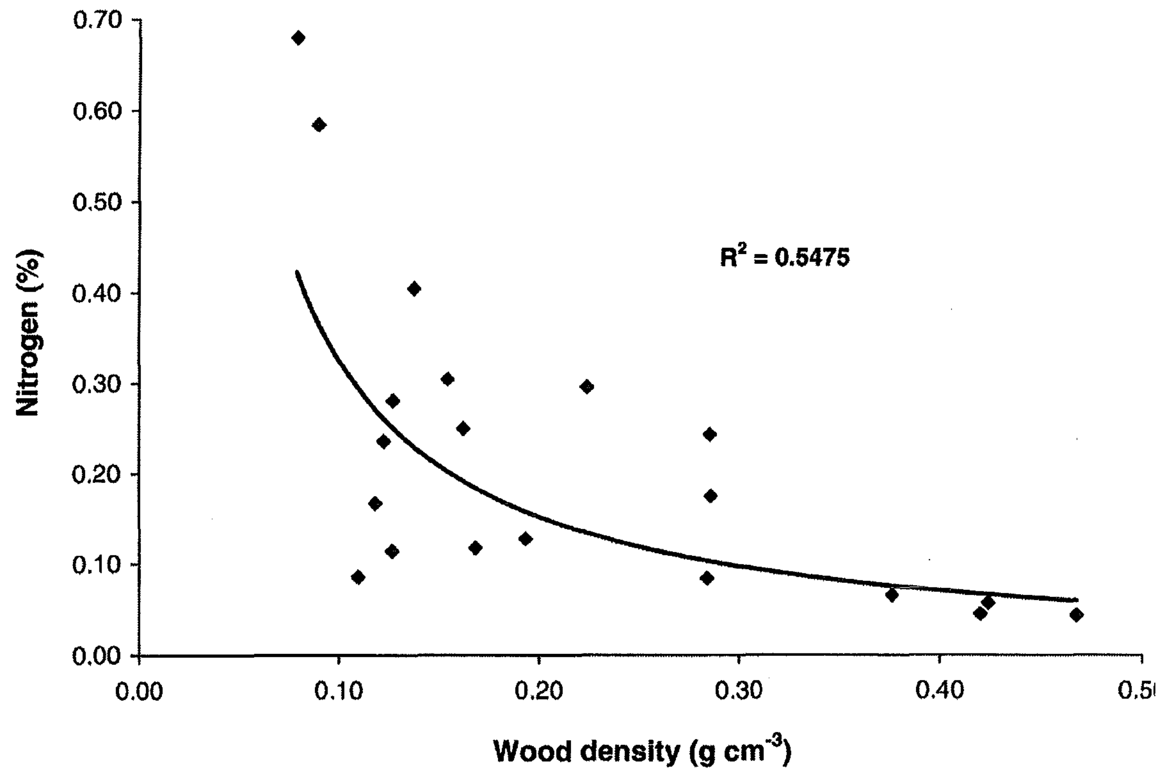

Figure 5. Relationship of percent nitrogen to wood density for decay class I and III down boles, red spruce and Fraser fir combined NDW, GRSM, 1994.

Table 4. Carbon and nitrogen pools for Fraser fir, red spruce, and yellow birch in the NDW, GRSM, 1994 (n = 50 plots). Sample statistics are the mean and the standard deviation in parentheses.

	Live	Standing Dead	Down Dead
Fraser Fir			
Nitrogen (kg ha^{-1})	0.94 (2.06)	25.70 (17.94)	25.51 (21.54)
Carbon (Mg ha^{-1})	0.59 (1.29)	8.75 (6.50)	7.62 (5.97)
Red Spruce			
Nitrogen (kg ha^{-1})	72.91 (34.81)	20.13 (25.46)	20.66 (18.59)
Carbon (Mg ha^{-1})	77.22 (36.86)	9.08 (11.71)	7.06 (6.50)
Yellow Birch			
Nitrogen (kg ha^{-1})	34.52 (46.58)	3.48 (8.47)	6.02 (11.56)
Carbon (Mg ha^{-1})	15.95 (21.52)	0.96 (2.62)	1.46 (2.81)
All[a]			
Nitrogen (kg ha^{-1})	108.37 (44.27)	49.31 (31.71)	52.20 (32.22)
Carbon (Mg ha^{-1})	93.76 (33.70)	18.79 (13.35)	16.14 (9.74)

[a] All refers to the summation of values for Fraser fir, red spruce, and yellow birch, only.

Table 5. Nitrogen pools in the NDW, GRSM, 1994 (n = 50 plots).

	Nitrogen (kg ha^{-1})	% of Total
Live Tissue		
Foliage	182.3[a]	31
Branch	90.8[a]	15
Bark	106.8[a]	18
Bole	108.4	18
Total Live	488.3	83
Dead Wood[b]		
Standing	49.31	8
Down	52.2	9
Total CWD	101.5	17
Grand Total	589.8	100

[a] From Barker et al. (2002)

[b] Only includes values for Fraser fir, red spruce, and yellow birch

woolly adelgid have resulted in a dense stand of regeneration of spruce and fir trees where canopy gaps exist (Witter and Ragenovich 1986; Nicholas et al. 1992b). These seedlings and saplings provide a sink for nitrogen, because plant nitrogen uptake depends on the vigor and successional stage of the forest (Fenn et al. 1998; Barker et al. 2002). Rapidly growing young trees depend more on the soil for nitrogen and are more effective at retaining nitrogen in plant biomass than older trees (Fenn et al. 1998). Between 1993 and 1998, nitrogen in live fir trees, in the NDW, increased from 7.8 kg ha^{-1} to 15.2 kg ha^{-1}, a 96% increase over a 5-year period (Barker et al. 2002). While net immobilization likely occurred in dead wood, this study found only a slight increase in nitrogen content over decay classes for Fraser fir and for red spruce boles. Due to the fact that nitrogen content in yellow birch increased more than in the other species (118% compared to 41% for Fraser fir), yellow birch boles were substantial sinks for nitrogen, which may be of greater significance in ecosystems with a higher proportion of this species.

An investigation into whether CWD was acting as a net sink or source for nitrogen at any given time during the decay process resulted in estimates for a critical C/N value for the major species in each decay class (Creed et al. 2004b). According to those critical C/N ratios, the majority of boles in the NDW were acting as sinks for nitrogen. Given that most logs were above the critical C/N ratio and the dense stand of regeneration that exists, there may be a temporary, albeit small, offset of nitrogen saturation in the NDW. The high degree of spatial heterogeneity of CWD may result in plot to plot differences in this offset; however, it is unknown what effect this variability would have at the watershed level. In the absence of another pulse to the system, once the majority of the CWD decays (18 years for 50% and 75 years for 95% of dead red spruce and Fraser fir; A. Rose, unpubl. data), uptake by regeneration may have slowed, and any benefits to the system from the offset of nitrogen will no longer be apparent.

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LITERATURE CITED

Aber, J.D., W. McDowell, K.J. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. BioScience 48:921-934.

Aber, J.D., K.J. Nadelhoffer, P. Steudler, and J.M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39:378-386.

Ågren, G.I., and E. Bosatta. 1988. Nitrogen saturation of terrestrial ecosystems. Environmental Pollution 54:185-197.

Alban, D.H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23:1744-1749.

Arthur, M.A., and T.J. Fahey. 1990. Mass and nutrient content of decaying boles in an Englemann spruce – subalpine fir forests, Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 20:730-737.

Barker, M., H. Van Miegroet, N.S. Nicholas, and I.F. Creed. 2002. Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce-fir watershed. Canadian Journal of Forest Research 32:1741-1752.

Bingham, B.B., and J.O. Sawyer, Jr. 1988. Volume and mass of decaying logs in an upland old-growth redwood forest. Canadian Journal of Forest Research 18:1649-1651.

Boggs, J.L., S.G. McNulty, M.J. Gavazzi, and J.M. Myers. 2005. Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forest. Canadian Journal of Forest Research 35:1901-1913.

Brady, N.C., and R.R. Weil. 1996. The Nature and Properties of Soils. Prentice-Hall, Upper Saddle River, N.J.

Brown, S., J. Mo, J.K. McPherson, and D.T. Bell. 1996. Decomposition of woody debris in Western Australian forests. Canadian Journal of Forest Research 26:954-966.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Science Society of America Journal 58:221-227.

Clark, D.F., D.D. Kneeshaw, P.J. Burton, and J.A. Antos. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Canadian Journal of Forest Research 28:284-290.

Creed, I.F., D.L. Morrison, and N.S. Nicholas. 2004a. Is coarse woody debris a net sink or source of nitrogen in the red spruce – Fraser fir forest of the southern Appalachians, U.S.A.? Canadian Journal of Forest Research 34:716-727.

Creed, I.F., K.L. Webster, and D.L. Morrison. 2004b. A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. Canadian Journal of Forest Research 34:744-753.

Daniels, L.D., J. Dobry, K. Klinka, and M.C. Feller. 1997. Determining year of death of logs and snags of Thuja plicata in southwestern coastal British Columbia. Canadian Journal of Forest Research 27:1132-1141.

Dull, C.W., J.D. Ward, H.D. Brown, G.W. Ryan, W.H. Clerke, and R.J. Uhler. 1988. Evaluation of spruce and fir mortality in the southern Appalachian mountains. R-8-PR13, U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, Ga.

Eagar, C. 1978. Distribution and characteristics of balsam woolly aphid infestations in the Great Smoky Mountains. M.S. thesis, University of Tennessee, Knoxville.

Eagar, C. 1984. Review of the biology and ecology of the balsam woolly aphid in southern Appalachian spruce-fir forests. Pp. 36-50 in P.S. White, ed., The southern spruce-fir ecosystem: its biology and threats. SER-71, U.S. Department of the Interior, National Park Service, Southeastern Research/Resources Management, Atlanta, Ga.

Edmonds, R.L., and J.L. Marra. 1999. Decomposition of woody material: nutrient dynamics, invertebrate/fungi relationships and management in Northwest forests. Pp. 68-79 in R.T. Meurisse, W.G. Ypsilantis, and C. Seybold, eds., Pacific Northwest Forest and Rangeland Soil Organism: Symposium Proceedings. PNW-GTR-461, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Ore.

Erickson, H.E., R.L. Edmonds, and C.E. Peterson. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Canadian Journal of Forest Research 15:914-921.

Fenn, M.E., M.A. Poth, J.D. Aber, J.S. Baron, B.T. Bormann, D.W. Johnson, A.D. Lemly, S.G. McNulty, D.F. Ryna, and R. Stottlemyer. 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. Ecological Applications 8:706-733.

Fernandez, I.J. 1992. Characterization of eastern U.S. spruce-fir soils. Pp. 40-63 in C. Eagar and M.B. Adams, eds., Ecology and Decline of Red Spruce in the Eastern United States. Springer-Verlag, New York.

Foster, J.R., and G.E. Lang. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Canadian Journal of Forest Research 12:617-626.

Garten, C.T., and H. Van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural 15N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research 24:1636-1645.

Grier, C.C. 1978. A Tsuga heterphylla-Picea sitchensis ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Canadian Journal of Forest Research 8:198-206.

Harmon, M.E., K. Cromack, Jr., and B.G. Smith. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Canadian Journal of Forest Research 17:1265-1272.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Harmon, M.E., T. Hennessy, and D.G. Silsbee. 1983. Woody fuel dimensions within Great Smoky Mountains National Park. SER-31, U.S. Department of the Interior, National Park Service, Southeastern Research/Resources Management, Atlanta, Ga.

Harper, K.A., C. Boudreault, L. De Grandpre, P. Drapeau, S. Gauthier, and Y. Bergeron. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environmental Review 11:79-98.

Hely, C., Y. Bergeron, and M.D. Flannigan. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Canadian Journal of Forest Research 30:674-687.

Husch, B., C.I. Miller, and T.W. Beers 1972. Forest Mensuration, 2nd ed. The Ronald Press, New York.

Johnson, D.W., S.E. Lindberg, and L.F. Pitelka. 1992. Atmospheric deposition and forest nutrient cycling, an introduction. Pp. 1-7 *in* D.W. Johnson and S.E. Lindberg, eds., Atmospheric Deposition and Forest Nutrient Cycling. Springer-Verlag, New York.

Johnson, D.W., H. Van Miegroet, S.E. Lindberg, D.E. Todd, and R.B. Harrison. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. Canadian Journal of Forest Research 21:769-787.

Joslin, J.D., J.M. Kelly, and H. Van Miegroet. 1992. Soil chemistry of North American spruce-fir stands: evidence for recent change. Journal of Environmental Quality 21:12-30.

Joslin, J.D., and M.H. Wolfe. 1992. Red spruce soil solution chemistry and root distribution across a cloud water deposition gradient. Canadian Journal of Forest Research 22:893-904.

Joslin, J.D., and M.H. Wolfe. 1994. Foliar defencies of mature southern Appalachian red spruce determined from fertilizer trials. Soil Science Society of America Journal 58:1572-1579.

Keenan, R.J., C.E. Prescott, and J.P. Kimmins. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. Canadian Journal of Forest Research 23:1052-1059.

Krankina, O.N., M.E. Harmon, and A.V. Griazkin. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Canadian Journal of Forest Research 29:20-32.

Laiho, R., and C.E. Prescott. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorous cycles in three Rocky Mountain coniferous forests. Canadian Journal of Forest Research 29:1592-1603.

Lambert, R.L., G.E. Lang, and W.A. Reiners. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forests. Ecology 61:1460-1473.

Lang, G.E., C.S. Cronan, and W.A. Reiners 1981. Organic matter and major elements of the forest floors and soils in subalpine balsam fir forest. Canadian Journal of Forest Research 11:388-399.

Lovett, G.M. 1992. Nitrogen chemistry, deposition, and cycling in forests: atmospheric deposition and canopy interactions of nitrogen. Pp. 152-165 in D.W. Johnson and S.E. Lindberg, eds., Atmospheric Deposition and Forest Nutrient Cycling. Springer-Verlag, New York.

McNulty, S.G., and J.D. Aber. 1993. Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation spruce-fir stand. Canadian Journal of Forest Research 23:1252-1263.

Naesset, E. 1999. Decomposition rate constants of Picea abies logs in southeastern Norway. Canadian Journal of Forest Research 29:372-381.

Nicholas, N.S. 1992. Stand structure, growth, and mortality in southern Appalachian spruce-fir. Ph.D. diss., Virginia Polytechnic Institute and State University, Blacksburg.

Nicholas, N.S. 1994. Sampling methodology: measuring live and dead biomass on spruce-fir permanent plots for the summer of 1994. Internal report, Tennessee Valley Authority, Norris.

Nicholas, N.S., and P.S. White. 1985. The effect of balsam woolly aphid infestation on fuel levels in spruce-fir forests of Great Smoky Mountains National Park. SER-74, U.S. Department of the Interior, National Park Service, Southeastern Research/Resources Management, Atlanta, Ga.

Nicholas, N.S., S.M. Zedaker, and C. Eagar. 1992a. A comparison of overstory community structure in three southern Appalachian spruce-fir forests. Bulletin of the Torrey Botanical Club 119:316-332.

Nicholas, N.S., S.M. Zedaker, C. Eagar, and F.T. Bonner. 1992b. Seedling recruitment, and stand regeneration in spruce-fir forests of the Great Smoky Mountains. Bulletin of the Torrey Botanical Club 119:289-299.

Nodvin, S.C., H. Van Miegroet, S.E. Lindberg, N.S. Nicholas, and D.W. Johnson. 1995. Acidic deposition, ecosystem processes, and nitrogen saturation in a high elevation southern Appalachian watershed. Water, Air, and Soil Pollution 85:1647-1652.

Pauley, E.F., S.C. Nodvin, N.S. Nicholas, A.K. Rose, and T.B. Coffey. 1996. Vegetation, biomass, and nitrogen pools in a spruce-fir forest of the Great Smoky Mountains National Park. Bulletin of the Torrey Botanical Club 123:318-329.

Pedlar, J.H., J.L. Pearce, L.A. Venier, and D.W. McKenney. 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecology and Management 158: 189-194.

Pyle, C., and M.P. Schafale. 1988. Land use history of three spruce-fir forest sites in Southern Appalachia. Journal of Forest History 32:4-21.

SAS Institute. 1990. SAS/STAT user's guide, version 6. SAS Institute, Cary, N.C.

Schlesinger, W.H. 1991. Biogeochemistry: an Analysis of Global Change. Academic Press, San Diego, Calif.

Shubzda, J., S.E. Lindberg, C.T. Garten, and S.C. Nodvin. 1995. Elevational trends in the fluxes of sulfur and nitrogen in throughfall in the southern Appalachian mountains: some surprising results. Water, Air, and Soil Pollution 85:2265-2270.

Sollins, P., S.P. Cline, T. Verhoeven, D. Sachs, and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17:1585-1595.

Stoddard, J.L. 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. Pp. 224-284 in L.A. Baker, ed., Environmental Chemistry of Lakes and Reservoirs. ACS-237, American Chemical Society, Washington, D.C.

Sturtevant, B.R., J.A. Bissonette, J.N. Long, and D.W. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7:702-712.

Tritton, L.M., and T.G. Siccama. 1990. What proportion of standing trees in forests of the Northeast are dead? Bulletin of the Torrey Botanical Club 117:163-166.

Van Miegroet, H., I.F. Creed, N.S. Nicholas, D.G. Tarboton, K.L. Webster, J. Shubzda, B. Robinson, J. Smoot, D.W. Johnson, S.E. Lindberg, G. Lovett, S. Nodvin, S. Moore. 2001. Is there synchronicity in N input and out fluxes at the Noland Divide Watershed, a small N-saturated forested catchment in the Great Smoky Mountains National Park. The Scientific World 1:480-492 (E-Journal).

Van Miegroet, H., D.W. Johnson, and D.E. Todd, 1993. Foliar response of red spruce saplings to fertilization with Ca and Mg in the Great Smoky Mountains National Park. Canadian Journal of Forest Research 23:89-95.

Van Miegroet, H., G.M. Lovett, and D.W. Cole. 1992. Nitrogen chemistry, deposition, and cycling in forests: conclusions. Pp. 202-207 in D.W. Johnson and S.E. Lindberg, eds., Atmospheric Deposition and Forest Nutrient Cycling. Springer-Verlag, New York.

Webster, C.R., and M.A. Jenkins. 2005. Coarse woody debris dynamics in the southern Appalachians as affected by topographic position and anthropogenic disturbance history. Forest Ecology and Management 217:319-330.

Witter, J.A., and I.R. Ragenovich. 1986. Regeneration of Fraser fir at Mt. Mitchell, North Carolina, after depredations by the balsam woolly adelgid. Forest Science 32:585-594.