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Contribution of Dead Wood to Biomass and Carbon Stocks in the Caribbean: St. John, U.S. Virgin Islands

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ABSTRACT

Dead wood is a substantial carbon stock in terrestrial forest ecosystems and hence a critical component of global carbon cycles. Given the limited amounts of dead wood biomass and carbon stock information for Caribbean forests, our objectives were to: (1) describe the relative contribution of down woody materials (DWM) to carbon stocks on the island of St. John; (2) compare these contributions among differing stand characteristics in subtropical moist and dry forests; and (3) compare down woody material carbon stocks on St. John to those observed in other tropical and temperate forests. Our results indicate that dead wood and litter comprise an average of 20 percent of total carbon stocks on St. John in both moist and dry forest life zones. Island-wide, dead wood biomass on the ground ranged from 4.55 to 28.11 Mg/ha. Coarse woody material biomass and carbon content were higher in moist forests than in dry forests. No other down woody material components differed between life zones or among vegetation categories ($P > 0.05$). Live tree density was positively correlated with fine woody material and litter in the moist forest life zone ($R = 0.57$ and 0.84, respectively) and snag basal area was positively correlated with total down woody material amounts ($R = 0.50$) in dry forest. Our study indicates that DWM are important contributors to the total biomass and, therefore, carbon budgets in subtropical systems, and that contributions of DWM on St. John appear to be comparable to values given for similar dry forest systems.

Key words: carbon; Caribbean forests; down woody material; subtropical forests.

THE IMPORTANCE OF DEAD WOOD IN NUTRIENT CYCLING, SOIL DEVELOPMENT, WILDLIFE HABITAT, and as a substrate for plant growth has been noted by many researchers (Maser *et al.* 1979, Harmon *et al.* 1986, Bull *et al.* 1997). Additionally, in areas where dry conditions, high winds, and weather-related disturbances facilitate the initiation and spread of wildfires, the amount and arrangement of dead wood on the landscape is critical information for land managers (Rollins *et al.* 2004). The demand for information regarding dead wood, its contribution to forest biomass and carbon cycling, and factors influencing the location of dead wood at a landscape scale have resulted in numerous studies in temperate forests where dead wood can contribute a relatively large percentage of aboveground biomass (AGB; Grier & Logan 1977). In contrast, there is a relative paucity of information regarding dead wood in tropical ecosystems, where scientists are beginning to study and report on the variation in dead wood between broad forest types, the contribution of dead wood to total AGB, and the role of dead wood in local and global carbon cycling (Weaver 1996, Clark *et al.* 2002, Nascimento & Laurance 2002).

Given the importance of dead wood biomass and carbon in the global carbon cycle and the limited amounts of such information for Caribbean forests, our goal was to fill knowledge gaps in current Caribbean carbon and biomass literature by: (1) describing the relative contribution of down woody materials (DWM; defined as woody plant material no longer supporting growth, not self-supporting, and lying on the ground) to carbon stocks on the island of St. John; (2) comparing these contributions across subtropical dry and moist forests of varying structure and composition; and (3) comparing DWM carbon stocks on St. John to those observed in other tropical forests.

METHODS

STUDY SITE.—The island of St. John, U.S. Virgin Islands, is located in the Caribbean Sea (13°22′ N, 64°40′ W) *ca* 90 km east of Puerto Rico. St. John is *ca* 5180 ha in area and covers rugged terrain ranging in elevation from sea level to 387 m asl, and slopes > 30 percent across 80 percent of the island (Rankin 2002). The climate is subtropical, with steady northeasterly tropical trade winds, seasonal rainfall, and periodic hurricanes. Precipitation ranges from 890 to 1400 mm/yr, and averaged 1141 mm/yr for the years 1971 to 2000 at the Cruz Bay weather station at the west end of the island (Weaver & Chinea-Rivera 1987, Southeast Regional Climate Center 2005). The majority of rainfall on St. John occurs during late spring, summer, and early fall, with a dry season from December through April (Weaver & Chinea-Rivera 1987). In recent history, hurricanes Hugo (1989) and Marilyn (1995) passed over the U.S. Virgin Islands, impacting the vegetation communities on St. John. Hurricane Marilyn passed through St. John with wind gusts of

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161–177 km/h, primarily impacting the south coast and mountain peaks. The north coast received minor damage consisting primarily of tree defoliation (U.S. Department of Commerce 1996).

Since the Danish colonization in 1718, the island's forests have been heavily impacted by colonial era agricultural practices such that no primary forest remains today (Acevedo-Rodriquez 1996, Woodbury & Weaver 1997). Agricultural activities were slowly abandoned in the late 1800s, and fallow fields and pastures began reverting to forest. Socioeconomic changes that allowed for forest recovery continued with the purchase of the U.S. Virgin Islands by the United States in 1917, and the establishment of the Virgin Islands National Park in 1956, which occupies over half of the island.

Forest vegetation on St. John consists of mangrove forests, subtropical moist upland, gallery and moist basin forests, and subtropical dry evergreen forests (Acevedo-Rodriquez 1996, Woodbury & Weaver 1997). Subtropical dry forest (hereafter 'dry forest') is found at elevations below 300 m with 600–1100 mm annual precipitation (Ewel & Whitmore 1973, Gibney *et al.* 2000). The dry forest canopy usually does not exceed 15–20 m in height, consisting of sparse treecrowns that are often deciduous and commonly with small, succulent, or leathery leaves (Woodbury & Weaver 1987, Gibney *et al.* 2000). The lower, understory vegetation of the Caribbean dry forest commonly consists of grasses, thorny legumes, and cacti. Some of the native tree species that are common to dry forest on St. John are gumbo limbo (*Bursera simaruba* [L.] Sarg.), torchwood (*Amyris elemifera* L.), Jamaican caper (*Capparis cynophallophora* L.), black manjack (*Cordia ricksecker*i Millsp.), water mampoo (*Pisonia subcordata* Sw.), lignumvitae (*Guaiacum officinale* L.), frangipani (*Plumeria alba* L.), and fustic (*Pictetia aculeata* [Vahl] Urban). The more heavily disturbed dry forest areas have numerous individuals of smaller-stemmed white leadtree (*Leucaena leucocephala* [Lam.] deWit), mesquite (*Prosopis juliflora* [Sw.] DC.) and porknut (*Acacia macracantha* Humb. & Bonpl.). Sweet acacia (*Acacia farnesiana* [L.] Willd.), tamarind (*Tamarindus indica* L.) and soapberry (*Melicoccus bijugatus* Jacq.) are found in moister areas. Subtropical moist forests (hereafter 'moist forest') are found in areas with 1100–2200 mm annual precipitation, with a 2- to 4-mo dry period (Gibney *et al.* 2000). These rainfall levels are found at the higher elevations on all three U.S. Virgin Islands where the hills and mountains intercept moisture carried on trade winds. Natural indicator species of moist forests include Guadeloupe marlberry (*Ardisia obovata* Desv. ex Hamilton), cabbagebark tree (*Andira inermis* [W. Wright] Kunth ex DC.), caimito de perro (*Chrysophyllum pauciflorum* Lam.), black mampoo (*Guapira fragrans* [Dum.-Cours.] Little), yellow mombin (*Spondias mombin* L.), sacky sac bean (*Inga laurina* [Sw.] Willd.), lancewood (*Nectandra coriacea* [Sw.] Griseb.), stinkingtoe (*Hymenaea courbaril* L.), and white cedar (*Tabebuia heterophylla* [DC.] Britt.)(Acevedo-Rodriquez 1996).

SAMPLE DESIGN AND FIELD MEASURES.—Dead wood, vegetation, and environmental data were collected from June through July of 2004 using the USDA Forest Service Forest Inventory and Analysis (FIA) sample design (USDA Forest Service 2003). To minimize any potential effects of seasonality, we sampled at the midpoint of the rainy season—the point at which any seasonal growth flushes would have already occurred but drought would not have resulted in senescence. Twenty plots were arranged on an unbiased, systematic sample grid across public and private land on St. John. The grid on St. John was composed of hexagons covering *ca* 200 ha each, with one sample plot located within each hexagon. Plots were located and mapped using global positioning system (GPS) equipment to ensure a high degree of accuracy. Plots were installed and measured where there was at least 10 percent tree canopy coverage and a minimum forested area of 0.4 ha around each plot center, as designated by USDA Forest Service FIA sample design guidelines. Plots consisted of a cluster of four subplots each with a 7.3-m radius. Each subplot had an area of 167 m^2, for a total sampled area of 670 m^2 (0.07 ha) per plot, or an island-wide sample of 1.2 ha (Fig. 1). Plots were assigned to life zones *sensu* Holdridge (1967).

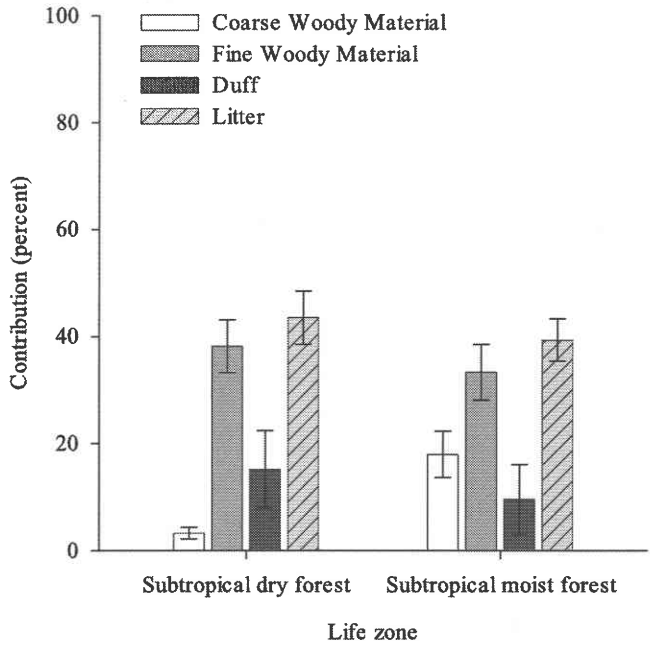

FIGURE 1. Contribution of individual components to total DWM biomass by Holdridge life zone.

Field crews collected forest inventory, understory structure and composition, and physiographic data on each subplot. Diameter at breast height (dbh) (taken at 1.37 m), total height, and other parameters were measured on all trees with dbh $\geq$ 12.5 cm within the subplots (see USDA Forest Service 2002 for a complete list of parameters). Diameter at breast height and total height were measured on saplings with dbh $\geq$ 2.5 cm within a 2.1-m-radius microplot nested in each subplot (USDA Forest Service 2002, Bechtold & Scott 2005).

Coarse and fine woody materials (CWM and FWM, respectively) were sampled on 7.32-m horizontal distance transects radiating from each FIA subplot center at 30, 150, and 270 degrees (Woodall & Williams 2005). FWM (1-, 10-, and 100-h fuels) were sampled on the 150-degree transect on each subplot (Burgan 1988). Transect diameter was defined as the diameter of a down woody

piece at the point of intersection with a sampling transect. FWM with transect diameters of 0.03–0.6 cm and 0.6–2.4 cm (1 and 10 h, respectively) was tallied separately on a 1.8-m slope distance transect (4.3–6.1 m on the 150-degree transect). FWM with transect diameters of 2.5–7.6 cm (100 h) was tallied on a 3.0-m slope distance transect (4.3–7.3 m on the 150-degree transect). CWM was defined by the FIA program as down logs with a transect diameter > 7.6 cm and a length > 91.4 cm. Transect diameter, length, small-end diameter, large-end diameter, decay class, species, evidence of fire, and presence of cavities were collected for every coarse woody piece encountered on each of the three 7.32-m transects on every forested FIA subplot. Duff and litter depth measurements were collected at the ends of each 7.32-m transect on forested FIA subplots. Duff was defined as decomposing leaves and other organic material containing no recognizable plant parts. Litter was defined as the loose plant material found on the top surface of the forest floor, not including bark or elements that meet the definitions of FWM or CWM.

DOWN WOODY MATERIAL CARBON AND BIOMASS ESTIMATION.—Line intersect estimation model-based estimators were used to determine volume and biomass of DWM for each inventory plot (Van Wagner 1964, Brown 1974, De Vries 1986). CWM and FWM carbon (C) content was estimated using a combination of line-intersect biomass per unit area estimators and C content conversion factors (Woodall & Williams 2005). Carbon content was then determined by multiplying mass estimates by a conversion factor (Birdsey 1992, Waddell 2002). Carbon in CWM (C_{CWM}) was calculated using equation 1

$$C_{CWM} = \sum_{1}^{n} cf\,G\left(\frac{\pi}{2L}\right)\left(\frac{V_m}{l_i}\right), \tag{1}$$

where n is the number of pieces, c is the proportion of carbon in the mass of the piece, f is the conversion factor for unit area values (10,000), G is the specific gravity of the piece (g/m^3), reduced by the necessary decay reduction factor, L is the total horizontal length (corrected for slope) of the transect (m), V_m is the volume of an individual piece (m^3), and l_i is the length of the individual piece i in meters (Woodall & Williams 2005). Birdsey (1992) provides carbon proportion factors (c) for hardwood (0.491) species types. Waddell (2002) provides decay reduction factors for various CWM decay classes for reducing the specific gravity of CWM pieces based on the state of decay.

Carbon storage in FWM (C_{FWM}) was calculated using equation (2)

$$C_{FWM} = \frac{(Gacsk)}{L} n_i \bar{d}_i^2, \tag{2}$$

where G is the specific gravity of the piece (g/m^3), a is the nonhorizontal lean angle correction factor for FWM pieces, c is the proportion of carbon in the FWM, s is the slope correction factor since FWM is measured along a slope distance transect, k is a constant representing a unit conversion, L is the slope length of the transect (m), n_i is the number of pieces of FWM in size class i, and $\bar{d}_i$ is the mean diameter (cm) of pieces within size class i. However, since species data are not collected for FWM, we assigned the mean value of the carbon proportions for softwoods and hardwoods (0.506) to c. For further information regarding the sample protocol and estimation procedures for the DWM sampled by the FIA program, see Woodall and Williams (2005).

ABOVEGROUND AND BELOWGROUND LIVE TREE BIOMASS ESTIMATION.—Aboveground biomass was calculated for all living trees with dbh ≥ 2.5 cm using the biomass equations developed by Brandeis *et al.* (2006) from data collected in Puerto Rico and the U.S. Virgin Islands for dry forest, moist forest, and gregorywood (*Bucida buceras* L.), where D_{bh} = diameter at breast height (1.37 m); H_T = total tree height, and AGB = total aboveground biomass in oven-dry kilograms, and BGB = belowground biomass.

$$\text{Subtropical moist forest} \quad \text{AGB} = e^{(-1.71904 + 0.78214 \times \ln D_{bh}^2 H_T)} \tag{3}$$

$$\text{Subtropical dry forest} \quad \text{AGB} = e^{(-1.94371 + 0.84134 \times \ln D_{bh}^2)} \tag{4}$$

$$\text{Bucida buceras} \quad \text{AGB} = e^{(-1.76887 + 0.86389 \times \ln D_{bh}^2)}. \tag{5}$$

The equation for Sierran palm (*Prestoea montana* [Graham] Nichols.) developed by Frangi and Lugo (1985) in Puerto Rico and recommended by Brown (1997) was used for estimating biomass in all palms.

$$\text{All palms} \quad \text{AGB} = 10.0 + 6.4 \times H_T. \tag{6}$$

Belowground biomass (BGB) was derived using the equation in Cairns *et al.* (1997) for estimating BGB for tropical forests.

$$\text{Belowground biomass} \quad \text{BGB} = e^{(-1.0587 + 0.8836 \ln AGB)} \tag{7}$$

A digitized map of the island's Holdridge life zones was used to assign each inventory sampling point to either dry or moist forest life zones as defined above, and the classification was confirmed by field crews and examination of the data so that the appropriate equation could be used in estimating AGB. Note that all of the biomass equations estimate total tree AGB in oven-dry kilograms from ground level to the tip of the tree, including stem, branch, and foliage. AGB and BGB estimates were summed for a total tree biomass estimate. Total tree biomass was multiplied by 0.5 for an estimate of carbon sequestered in each tree (Nabuurs *et al.* 2003).

ANALYTICAL METHODS.—We used mixed model analysis of variance (ANOVA) in SAS version 8.0 to determine if differences in biomass and carbon content occurred between moist and dry forest. Differences were recognized at the alpha = 0.05 level. To further explore relationships between moist and dry forest stand characteristics and dead wood, we used Pearson correlations. Correlations were considered significant at $P = 0.05$.

To compare our results with other studies in the tropics and subtropics, we synthesized results from seven published studies throughout the Caribbean, Central America, and South America. We calculated a temperature/precipitation ratio for comparison between dry and moist forests following Murphy and Lugo (1986). Because studies were conducted at different scales in stands with widely varying characteristics, we developed an index of DWM to stand basal area by dividing total DWM carbon per hectare by mean basal area per hectare.

RESULTS

DEAD WOOD CONTRIBUTIONS TO BIOMASS AND CARBON.—Island-wide estimates of dead wood biomass on inventory plots (all DWM, standing dead wood, duff, and litter combined) averaged 13.3 Mg/ha ± 1.4 SE. (range = 4.6–28.3 Mg/ha). Down woody material biomass estimates (including coarse, fine, duff, and litter) averaged 12.6 Mg/ha ± 1.3 (4.6–28.1 Mg/ha). Standing dead AGB on all plots averaged 0.8 Mg/ha ± 0.2 (0.0–3.2 Mg/ha). Live woody AGB on all plots averaged 77.4 Mg/ha ± 6.7 (29.2–143.4 Mg/ha). Combined (live and dead) woody AGB averaged 78.1 Mg/ha ± 6.8 (29.2–143.4 Mg/ha).

Down woody material (including CWM, FWM, duff, and litter) contributed 6–46 percent of total AGB (live and dead), while standing dead wood contributed 0–6 percent of total woody AGB. On average, dead wood (standing and DWM) contributed 20 ± 3 percent of total woody AGB (range = 6–52 percent).

CWM made up 0–35 percent of total DWM, though 50 percent of the sample locations in dry forest did not contain any CWM. In comparison, FWM comprised 9–66 percent, duff comprised 0–71 percent, and litter comprised 12–73 percent of DWM (Fig. 1). Nearly all of the CWM fell into the 7.6–20 cm diameter class and was moderately decayed (*i.e.*, sound heartwood with soft or absent sapwood). Few freshly fallen, intact logs were recorded and no pieces in the most decomposed decay class (*i.e.*, rotten heartwood, piece no longer maintaining shape) were recorded.

Estimated total carbon (excluding soil and herbaceous vegetation) on St. John averaged 56.7 Mg/ha ± 4.2 SE. Dead woody materials contributed an estimated 16 percent (8.9 Mg/ha ± 0.8) of the total aboveground and belowground carbon on St. John. Litter on the forest floor contributed more carbon per hectare than either FWM or CWM, with a mean of 5.8 ± 0.6 Mg/ha. CWM contributed an average of 0.6 ± 0.2 Mg/ha, FWM contributed an average of 2.1 ± 0.2 Mg/ha, and snags (aboveground and belowground portions) contributed an average of 0.5 ± 0.2 Mg/ha. Dead wood and forest floor litter comprised 6–34 percent of total carbon (not including soil carbon or herbaceous vegetation).

COMPARISONS BY LIFE ZONE AND FOREST TYPE.—Mean quantities of estimated CWM were higher in moist forest than in dry forest (Table 1; $P = 0.004$). FWM, duff, and litter quantities did not differ between dry and moist forest (Table 1). Percent contributions of dead wood to total AGB did not differ between moist and dry forest.

Overall, total estimated carbon (aboveground and belowground combined, not including soils or herbaceous vegetation) was higher in moist forest than in dry forest ($P = 0.03$). Similarly, the amount of carbon contributed by standing dead trees and CWM was higher in moist forest than in dry forest ($P = 0.04$ and 0.004, respectively). Neither carbon contributed by FWM or forest floor litter differed between life zones.

DEAD WOOD AND STAND CHARACTERISTICS.—Total live tree basal area on St. John ranged from 7.5 to 40.0 m^2/ha. Basal area was higher in moist forest than in dry forest ($\mu = 16.6$ and 27.2, respectively; $P = 0.004$). Total (dry and moist forest combined) live tree basal area and volume were positively correlated with CWM, but were not correlated with duff, litter, or FWM (Table 2). Conversely, the number of trees per hectare was correlated with FWM island wide, but was not correlated with any other DWM variables.

Total standing dead tree (snag) basal area on St. John ranged from 0.0 to 1.3 m^2/ha and was slightly higher in moist forest than in dry forest ($\mu = 0.5$ and 0.1, respectively; $P = 0.07$). Snag basal area was highest in moist forest vegetation groups ($P = 0.03$), and was not observed in the disturbed dry forest. The number of snags per hectare and snag basal area were very strongly correlated with CWM island wide, but were not correlated with any other down woody variables (Table 2).

Correlations between forest dead wood and stand characteristics for moist and dry forests independently indicated that the number of live trees per hectare was strongly correlated with litter in moist forest (Table 2). Snag density and snag basal area were strongly correlated with CWM in dry forests. Conversely, CWM variables were not correlated with either dry or moist forest live tree density or live tree basal area.

DISCUSSION

The quantities of the various components that make up DWM in the forests of St. John were largely independent of life zone and vegetation class, except for CWM that was higher in moist forest. Stand correlations to CWM island wide (positive with live tree basal area and negative with stem density) make intuitive sense. Rubino and McCarthy (2003) found similar negative correlations between CWM and tree density in forests of southern Ohio, though interestingly that same study also showed negative correlations between basal area and CWM. Though overall carbon values do not differ, stand characteristics appear to play a role in the type of material present. Mature moist forests with fewer numbers of larger diameter trees contribute CWM to the carbon pool on St. John, while young moist forests with large numbers of small diameter trees primarily contribute FWM, litter, and duff to the carbon pool. Dry forests on St. John consist of dense thickets of small diameter trees, scrub, and cacti with very few, if any, large trees. These dry forests are contributing equitable amounts of FWM, duff, and litter with almost no CWM.

The strongest correlations between stand characteristics and DWM occurred between snag basal area and density and CWM.

TABLE 1. *Means (Mg per hectare) and standard errors of down woody material component biomass by life zones and vegetation group on St. John, U.S. Virgin Islands. Letters represent results of ANOVA mean separation tests. Groups with the same letters were not significantly different.*

	Down woody material component (± SE)				
Plot grouping	Coarse wood	Fine wood	Duff	Litter	All DWM
Holdridge life zone					
Subtropical moist forest (8)	2.23 (0.41)^{A}	4.60 (0.71)^{A}	1.01 (1.93)^{A}	5.32 (0.78)^{A}	13.16 (2.14)^{A}
Subtropical dry forest (12)	0.49 (0.34)^{B}	3.81 (0.58)^{A}	3.36 (1.58)^{A}	4.48 (0.64)^{A}	12.14 (1.74)^{A}
Island-wide	1.19 (0.32)	4.12 (0.45)	2.42 (1.23)	4.82 (0.50)	12.55 (1.32)

In both life zones high densities and/or basal areas of snags resulted in larger quantities of CWM and duff, and smaller quantities of FWM and litter. These somewhat intuitive relationships suggest that stands that experience disturbances resulting in tree mortality (*e.g.*, hurricane or other weather-related event) produce large amounts of DWM of all types initially then, over time, smaller woody material decomposes while CWM remains behind resulting in correlations like the ones we observed on St. John.

TABLE 2. *Correlations between stand characteristics and down woody material components by life zone on St. John, U.S. Virgin Islands. Groups with asterisks indicate significance at the* P = *0.05 level.*

	Down woody material component				
Sample (N)	Coarse wood	Fine wood	Duff	Litter	All DWM
St. John Island-Wide (20)					
Live tree basal area	0.49*	0.01	−0.10	0.15	0.09
Live tree density	−0.01	0.52*	−0.21	0.36	0.12
Live tree volume	0.64*	−0.25	−0.10	0.01	−0.02
Snag basal area	0.70*	−0.23	0.31	0.13	0.42
Snag density	0.77*	−0.12	0.17	0.18	0.37
Holdridge life zone					
Subtropical moist forest (8)					
Live tree basal area	0.46	−0.16	−0.24	0.14	0.05
Live tree density	−0.38	0.57	−0.49	0.84*	0.59
Live tree volume	0.67	−0.21	−0.13	−0.10	0.01
Snag basal area	0.54	−0.29	0.31	0.05	0.28
Snag density	0.59	−0.16	0.05	0.14	0.31
Subtropical dry forest (12)					
Live tree basal area	−0.18	−0.13	0.10	−0.01	0.05
Live tree density	−0.34	0.41	−0.08	−0.17	−0.07
Live tree volume	0.32	−0.67*	−0.00	−0.03	−0.12
Snag basal area	0.82*	−0.43	0.52	0.06	0.50
Snag density	0.81*	−0.45	0.51	0.05	0.48

We compared the contribution of DWM to carbon stocks on St. John to stocks described in published studies in tropical forests in the Caribbean and elsewhere in terms of gross amounts and amounts relative to forest basal area. Total DWM carbon stocks were divided by stand basal area to give a relative index of megagram of DWM carbon for each square meter of stand basal area (Table 3). Compared to other tropical forests in the Caribbean and elsewhere, forest structure and contributions of DWM on St. John appear to be comparable to values found in similar dry forests. Live tree basal area was lower for both dry and moist forests than the values reported by Murphy and Lugo (1995) for Central America and the Caribbean, but was similar to (though slightly lower than) pre-Hurricane Hugo values reported by Weaver (1996) for Cinnamon Bay Forest on St. John. Live AGB was also lower, on average, than the values reported by Weaver (1996), though values we calculated in moist forest were similar.

St. John's total litter values were similar to averages derived by Lugo and Brown (1982) through a synthesis of productivity studies in various tropical and subtropical life zones. Those authors also found that litterfall and litter storage tended to be higher in moist forests and lower in dry forests (Lugo & Brown 1982). Our estimates of the contribution of litter to total carbon storage were higher, but soil carbon and carbon contributed by live herbaceous plants was not included in our estimates. Lugo and Brown (1982) also reported higher AGB values in moist forest than in dry forest, as did our study. Murphy and Lugo (1986) note that in subtropical dry forests in Puerto Rico a large proportion of AGB (43%) is represented by vegetation other than woody species > 5 cm dbh, suggesting that even though we measured woody vegetation > 2.5 cm dbh, our study may still have missed a substantial pool of AGB in forested systems.

Duff and litter appeared to contribute more down woody biomass than coarse or FWM—an observation that contrasts with observations by Harmon *et al.* (1995), who note that pre-hurricane data from dry tropical forests in Mexico indicate that coarse and FWM biomass 'greatly exceeds the mass found in surface litter.' Litter biomass estimates were similar to, though slightly lower than, Weaver's (1996) estimate of 9.33 Mg/ha for average quantities of loose litter at Cinnamon Bay, St. John. Values for litter biomass quantities island wide (2.31–10.82 Mg/ha) were similar

TABLE 3. *Comparisons of St. John, U.S. Virgin Islands stand characteristics (mean ± SE) with other subtropical and tropical studies.*

Location (reference)	N[a]	T/P ratio[b]	No. of Stems/ha[c]	Basal area m^2/ha	Live tree AGB (Mg/ha)	Snag AGB (Mg/ha)	Total tree biomass (AGB + BGB)	Total DWM Carbon Mg/ha[d]	DWMC/ BA ratio
St. John, USVI: subtropical moist forest	8	1.6	6677 (2148)	26.7 (7.5)	94.0 (26.0)	1.3 (1.1)	115.8 (10.7)	8.9	43.4
St. John, USVI: subtropical dry forest	12	3.1	4984 (1659)	16.5 (6.8)	66.3 (28.0)	0.4 (1.0)	82.0 (9.9)	8.1	39.5
St. John Island-wide	20	2.3	5661 (448)	20.5 (1.9)	77.4 (6.7)	0.8 (0.2)	96.43 (8.16)	8.4	41.0
Cinnamon Bay, St. John, USVI (Weaver 1996)	16	2.4	3375 (–)	–	131.5 (–)	–	–	–	–
Puerto Rico Island-wide (Brandeis *et al.*, in press)	25	1.7	3160 (160)	20.9 (1.3)	86.4 (5.7)	2.0 (0.3)	105.46 (7.02)	21.5	102.7
Guanica Forest, Puerto Rico (Murphy & Lugo 1986)	15	2.9	12,173 (–)	17.8 (–)	–	1.9 (–)	98.00 (–)	7.5	42.2
Venezuela (Delaney *et al.* 1997)	23	1.3	–	–	134–520	–	400–1086	1.2–38.3	–
Manaus, Brazil (Nascimento & Laurence 2002)	20	1.1	–	–	346.6 (–)	6.1 (–)	–	35.3	–
La Selva, Costa Rica (Clark & Clark 2000; Clark *et al.* 2002)	18	0.7	504 (22)	23.6 (0.5)	160.5 (4.2)	6.5 (0.9)	–	23.2[e]	98.3
Rancho San Filipe, Mexico (pre-Hurricane Gilbert) (Harmon *et al.* 1995)	12	2.3	–	26.9 (0.9)	133 (6)	–	–	19.7[f]	73.2

[a]Sample plot sizes and designs vary by study.

[b]Temperature/precipitation ration *sensu* Murphy and Lugo 1986.

[c]Stems ≥2.5 cm for St. John and Puerto Rico, Brazil; stems ≥10 cm for Venezuela, Costa Rica, Mexico.

[d]Includes CWM, FWM, and litter.

[e]CWM only.

[f]Pre-hurricane CWM plus pre-hurricane FWM/leaf litter range minimum.

to pre-hurricane measurements from that study (4.22–6.47 Mg/ha; Whigham *et al.* 1991), but our coarse and FWM measurements were much lower than their combined woody biomass estimates of 17.7–42.7 Mg/ha (Harmon *et al.* 1995). The forests at Cinnamon Bay represent some of the more mature moist forests on the island (stand age = 125 yr; Ray & Brown 1995). Since mature forests may contain large fallen trees, and typically consist of larger trees that may shed more branches than young, small trees, the relative maturity of Cinnamon Bay in contrast with the overall forest landscape could explain the discrepancy between our CWM measurements and theirs. Additionally, our sample was not biased toward or against particular features on the landscape. Any feature meeting the FIA definition of 'forest' was included in the sample, so that the sample included both highly disturbed forests (edges, backyards, resort grounds) as well as mature forests like those at Cinnamon Bay and in some of the other studies mentioned.

Carbon contributed by DWM on St. John, even in moist forest, was low compared to some other studies in the tropics and subtropics (Table 3). Down woody material estimates from this study for the entire island of St. John were very similar to estimates given by Murphy and Lugo (1986) for the subtropical dry Guánica Forest in Puerto Rico, which has comparable temperature, precipitation, and total live tree basal area to dry forest on St. John. However, estimates from this study were much lower than island-wide estimates of DWM carbon on Puerto Rico (T. Brandeis, pers. obs.). Our live tree, litter, and dead wood carbon estimates are similar to mean and range values for very dry tropical forests (annual rainfall = 800 mm) in Venezuela, as given by Delaney *et al.* (1997). In contrast, mean fallen CWM biomass in tropical forests at the La Selva Biological Station in Costa Rica (46.3 Mg/ha; Clark *et al.* 2002), and in pre-hurricane-damaged dry forests on the Yucatan Peninsula (31 Mg/ha; Whigham *et al.* 1991; Harmon *et al.* 1995) were much higher than mean CWM biomass on St. John (1.19 Mg/ha), and the ratio of DWM carbon to basal area was lower on St. John, as well.

Relatively low contributions of DWM to carbon stocks on St. John might be due to the relative youth of forests that are still recovering from intensive human disturbance of colonial era agricultural practices or to the more recent disturbances caused by Hurricane

Hugo in the late 1980s and Hurricane Marilyn in the mid-1990s. Compared to continental tropical forests (Manaus and La Selva), Caribbean forests contain much less carbon in live and standing dead trees. In continental tropical forests like La Selva, much of the forest carbon is concentrated in far fewer, much larger trees. Hurricane-impacted Caribbean forests consist of smaller, shorter-stature trees due in part to their frequent disturbance and damage (Van Bloem *et al.* 2005). The Yucatan Peninsula study site, an area that is also impacted by hurricanes, however, showed far more DWM carbon in forests with very similar stand characteristics, perhaps indicating either a different land-use history, less-frequent hurricane disturbance, or both. Additionally, rapid decay rates associated with warm, humid climates likely play a role in the overall contribution of down wood to overall forest carbon. Though the contribution of soil to forest carbon was not addressed here, other studies have indicated that the contribution of soil organic carbon to total carbon stocks is high relative to the contribution of carbon by DWM, particularly in subtropical moist life zones, suggesting that attempts at soil carbon estimation are important future research needs for quantifying total carbon stocks on St. John and similar Caribbean landscapes (Brown & Lugo 1982, Delaney *et al.* 1997, Silver *et al.* 2004).

Our study indicates that DWM contributes an average of 16 percent of the total aboveground and belowground carbon (excluding herbaceous and soil carbon) on St. John. Live and dead tree basal area and volume are important factors in the quantity of CWM present on the forest floor, while stand density appears to strongly influence FWM and litter presence. Contributions of DWM on St. John appear to be comparable to values given for similar dry forest systems.

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LITERATURE CITED

ACEVEDO-RODRIQUEZ, P. 1996. Flora of St. John, U.S. Virgin Islands. The New York Botanical Garden, Bronx, New York, New York.

BECHTOLD, W. A., AND C. T. SCOTT. 2005. The forest inventory and analysis plot design. *In* W. A. Bechtold and P. L. Patterson (Eds.). The enhanced forest inventory and analysis program—national sampling design and estimation procedures, pp. 27–42. General Technical Report SRS–80. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina.

BIRDSEY, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. General Technical Report WO–59. 51 p. U.S. Department of Agriculture Forest Service, Washington, DC.

BRANDEIS, T. J., M. DELANEY, B. R. PARRESOL, AND L. ROYER. 2006. Development of equations for predicting Puerto Rican subtropical dry forest biomass and volume. For. Ecol. Manage. 233: 133–142.

BROWN, J. K. 1974. Handbook for inventorying downed woody material. General Technical Report INT–16. U.S. Department of Agriculture Forest Service, 24 p. Intermountain Forest and Range Experiment Station, Ogden, Utah.

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

BROWN, S., AND A. E. LUGO. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14: 161–187.

BULL, E. L., C. G. PARKS, AND T. R. TORGERSEN. 1997. Trees and logs important to wildlife in the interior Columbia River basin. General Technical Report PNW–391. 55 p. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.

BURGAN, R. E. 1988. 1988 Revisions to the 1978 national fire-danger rating system. Research Paper SE–273. 39 p. U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina.

CAIRNS, M. A., S. BROWN, E. H. HELMER, AND G. A. BAUMGARDNER. 1997. Root biomass allocation in the world's upland forests. Oecologia 111: 1–11.

CLARK, D. B., AND D. A. CLARK. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137: 185–198.

CLARK, D. B., D. A. CLARK, S. BROWN, S. F. OBERBAUER, AND E. VELDKAMP. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. For. Ecol. Manage. 164: 237–248.

DELANEY, M., S. BROWN, A. E. LUGO, A. TORRES-LEZAMA, AND N. B. QUINTERO. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. J. Trop. Ecol. 13: 697–708.

DE VRIES, P. G. 1986. Sampling theory for forest inventory: A teach-yourself course. Chapter 13: Line-intersect sampling, pp. 242–279. Springer-Verlag, Berlin, Germany.

EWEL, J. J., AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Research Paper ITF–18. 72 p. U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry, Río Piedras, Puerto Rico.

FRANGI, J. L., AND A. E. LUGO. 1985. Ecosystem dynamics of a subtropical floodplain forest. Ecol. Monogr. 55: 351–369.

GIBNEY, E., T. T. O'REILLY, AND B. DEVINE. 2000. USVI vegetation community classification System. The Virgin Islands data atlas series. The Nature Conservancy and Virgin Islands Conservation Data Center. Virgin Islands.

GRIER, C. C., AND R. S. LOGAN. 1977. Old-growth *Pseudotsuga menziesii* communities of a Western Oregon watershed: Biomass distribution and production budgets. Ecol. Monogr. 47: 373–400.

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 JR., AND K. W. CUMMINS. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

HARMON, M. E., D. F. WHIGHAM, J. SEXTON, AND I. OLMSTEAD. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. Biotropica 27: 305–316.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206 pp.

LUGO, A. E., AND S. BROWN. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14: 161–187.

MASER, C., R. G. ANDERSON, K. CROMACK Jr., J. T. WILLIAMS, AND R. E. MARTIN. 1979. Dead and down woody material. *In* J. W. Thomas (Ed.). Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington, pp. 78–95. Agriculture Handbook 553. U.S. Department of Agriculture Forest Service, Washington, DC.

MURPHY, P. G., AND A. E. LUGO. 1986. Ecology of tropical dry forest. Ann. Rev. Ecol. Syst. 17: 67–88.

MURPHY, P. G., and A. E. LUGO. 1995. Dry forests of Central America and the Caribbean. *In* S. H. Bullock, H. A. Mooney, AND E. Medina (Eds.). Seasonally dry tropical forests, pp. 9–34. Cambridge University Press, Cambridge, UK.

NABUURS, G. J., N. H. RAVINDRANATH, K. PAUSTIAN, A. FREIBAUER, W. HOHENSTEIN, AND W. MAKUNDI. 2003. LUCF sector good practice guidance. Chapter 3. *In* J. Penman, M. Gytarsky, T. Hiraishi, T. Krug, D. Kruger, R. Pipatti, L. Buendia, K. Miwa, T. Ngara, K. Tanabe, and F. Wagner (Eds.). Good practice guidance for land use, land-use change, and forestry, pp. 3.1–3.95. IPCC National Greenhouse Gas Inventories Program, Technical Support Unit.

NASCIMENTO, H. E. M., AND W. F. LAURANCE. 2002. Total aboveground biomass in central Amazonian rainforests: A landscape-scale study. For. Ecol. Manage. 168: 311–321.

RANKIN, D. W. 2002. Geology of St. John, U.S. Virgin Islands. 36 p. U.S. Department of the Interior, U.S. Geological Survey.

RAY, G. J., AND B. BROWN. 1995. The structure of five successional stands in a subtropical dry forest, St. John, U.S. Virgin Islands. Caribb. J. Sci. 31: 212–222.

ROLLINS, M. G., R. E. KEANE, AND R. A. PARSONS. 2004. Mapping fuels and fire regimes using remote sensing, ecosystem simulation, and gradient modeling. Ecol. Appl. 14: 75–95.

RUBINO, D. L., AND B. C. MCCARTHY. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. For. Ecol. Manage. 183: 221–238

SILVER, W. L., L. M. KUEPPERS, A. E. LUGO, R. OSTERTAG, AND V. MATZEK. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. Ecol. Appl. 14: 1115–1127.

SOUTHEAST REGIONAL CLIMATE CENTER. 2005. Southeast regional climate center (SERCC) climate information. http://www.sercc.com/climate-info/climate_info.html (accessed March 2006).

USDA FOREST SERVICE. 2002. Field procedures for Puerto Rico and the Virgin Islands, Supplement C to SRS Regional Manual 1.56. http://srsfia2.fs.fed.us/data_acquisition/manual.shtml. U.S. Department of Agriculture Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit, Knoxville, Tennessee.

USDA FOREST SERVICE. 2003. FIA field methods for phase 3 measurements, 2003, edition 1.7. http://www.fia.fs.fed.us/library/field-guides-methods-proc./ U.S. Department of Agriculture Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit, Knoxville, Tennessee.

U.S. DEPARTMENT OF COMMERCE. 1996. Natural disaster survey report: Hurricane Marilyn, September 15–16 1995. U.S. Department of Commerce, Washington, DC.

VAN BLOEM, S. J., P. G. MURPHY, A. E. LUGO, R. OSTERTAG, M. R. COSTA, I. R. BERNARD, S. M. COLÓN, AND M. C. MORA. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. Biotropica 37: 571–583.

VAN WAGNER, C. E. 1964. The line-intersect method in forest fuel sampling. For. Sci. 10: 267–276.

WADDELL, K. L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecol. Indust. 1: 139–153.

WEAVER, P. L. 1996. Forest productivity in the Cinnamon Bay watershed, St. John, U.S. Virgin Islands. Caribb. J. Sci. 32: 89–98.

WEAVER, P. L., AND J. D. CHINEA-RIVERA. 1987. A phytosociological study of Cinnamon Bay watershed, St. John, U.S. Virgin Islands. Caribb. J. of Sci. 23: 318–336.

WHIGHAM, D. F., I. OLMSTED, E. C. CANO, AND M. E. HARMON. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the Northeastern Yucatan Peninsula. Biotropica 23: 434–441.

WOODALL, C., AND M. S. WILLIAMS. 2005. Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program. General Technical Report NC–256. 47 p. U.S. Department of Agriculture Forest Service, North Central Research Station, St. Paul, Minnesota.

WOODBURY, R. O., AND P. L. WEAVER. 1987. The vegetation of St. John and Hassel island, U.S. Virgin Islands. Research/Resources Management Report SER–83. 103 pp. U.S. Department of the Interior, National Park Service, Atlanta, Georgia.

WOODBURY, R. O., AND P. L. WEAVER. 1997. The vegetation of St. John and Hassel island, U.S. Virgin Islands. U.S. Department of the Interior, National Park Service, Atlanta, Georgia.