Caribbean
Naturalist

No. 13 2014

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Ernesto Medina, Eileen H. Helmer, Elvia Meléndez-Ackerman, and Humfredo Marcano-Vega

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Cover Photograph: Abrupt cliffs facing the Sardinera beach at the western coast of Mona Island, bordered by a coastal woodland reaching the narrow coastal plain. These forests contain most of the species occurring on the island plateau, though here attaining larger sizes because of a more favorable fresh water supply. Photograph © Ernesto Medina.

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Natural Vegetation Groups and Canopy Chemical Markers in a Dry Subtropical Forest on Calcareous Substrate: The Vegetation of Mona Island, Puerto Rico

Ernesto Medina[1, 3,*], Eileen H. Helmer[1], Elvia Meléndez-Ackerman[2], and Humfredo Marcano-Vega[4]

Abstract - Mona Island is the third largest island in the archipelago of Puerto Rico located about 70 km west of the main island. Presently it is a wilderness refuge that contains well-preserved arboreal and shrubby vegetation, and distinct cactus forests, covering the calcareous, elevated plateau. During a forest inventory conducted by the US Forest Service, we obtained leaves of 53 species constituting the vegetation canopy on the plateau of Mona Island. We conducted a biochemical characterization of these leaves based on analyses of carbon (C), nitrogen (N), acid detergent fiber (cellulose, hemicellulose and lignin), and ash content with emphasis on the most abundant species. Four clusters of species were characterized by (1) relative high % N and low lignin, (2) high % C, low % ash, and cellulose + hemicellulose, (3) low % C and N, and high % ash, and (4) low % ash and high % lignin. These clusters overlapped partially with the characteristic species of physiognomic vegetation types previously described for the island. Cluster 2 species dominated the forest on the calcareous plateau, whereas cluster 3 species dominated forests on depressions. Shrublands were dominated by species in clusters 1 and 2. The data set of Mona Island species showed substantially higher average C/N ratios (probably indicating N limitation), and lower % lignin than species of tropical dry and humid forests. In addition, a large fraction of species had leaf traits associated with herbivore deterrence. The species in clusters 2 and 4 showed % C at ≈55%, indicating the accumulation of carbon-rich compounds such as lignin and lipids. This project was part of a larger one seeking to study tropical dry vegetation and understand functional types as well as their relationships with climate, canopy leaf chemistry, and remotely sensed imagery. The data set assembled and our findings regarding the association with vegetation types may serve as a baseline for evaluating climate-change processes.

Introduction

Global climate change is expected to lead to drier climatic conditions in much of Mesoamerica and the Caribbean (Neelin et al. 2006). Gradual changes in tropical forest function and species composition are possible outcomes of this drying, and approaches are needed to monitor and understand the implications of these effects. Forest inventories and remote sensing are powerful procedures to map and monitor

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Manuscript Editor: Bill Buck

changes in tropical dry forest habitats that may result from global climate change. However, we still need to build our framework for interpreting the inventory and remote sensing data.

Our study ran within the context of a larger project that seeks to analyze the spatial distribution of tropical dry forest functional types as well as the relationships between climate, canopy-leaf chemistry and remotely sensed imagery. To the extent that these are related, remote sensing with satellite imagery is one potential way to assess vegetation changes in tropical dry-forest habitats that may develop as a result of global climate change. Leaves of woody plants constitute the major component of forest canopies, and their structure and chemical composition varies widely among large taxonomic groups (gymnosperms compared to angiosperms), phenology types (deciduous compared to evergreens), and life forms (trees compared to shrubs) (Cochrane 2000). These variations profoundly influence the absorption and reflection of sunlight impinging upon plant canopies. For example, the preferential absorption of electromagnetic radiation between 600–700 nm (red), and reflection between 700–750 nm (near infrared), are related to the amount of chlorophyll present in the canopy and are the basis for the calculation of a canopy productivity index (normalized difference vegetation index [NDVI]). Data are collected from satellite or aerial imagery and the NDVI is calculated from measurements of reflected light spectra (Gitelson and Merzlyak 1997, Sellers 1985). Hyperspectral images are now used to estimate a variety of compounds in plant canopies (Asner and Martin 2008, 2009; Curran 1989; Martin and Aber 1997; Porder et al. 2005), and are being evaluated for their use in remote-sensing appraisals of canopy-specific diversity (Castro-Esau et al. 2006, Clark et al. 2005, Cochrane 2000).

In the present study, we sampled leaves of woody plant species of the Caribbean limestone island of Mona to determine their concentrations of ash, carbon (C), nitrogen (N), lignin, and (cellulose + hemicellulose [c+h]). Our objectives were to 1) characterize relationships among concentrations of these leaf components; 2) test whether we could develop a chemical classification of subtropical dry forest woody species on Mona Island based on leaf ash, C, N, lignin, and c+h; and 3) compare the distribution of the species and chemical groups identified here with previous studies on Mona forest-vegetation ecology and species distribution. Ecophysiological interpretations were based on averages per species without consideration of spatial distribution. These data may be used to evaluate canopy chemistry by extrapolating from vegetation-structure studies.

Field-site description

We sampled vegetation growing on the Mona Island plateau, which belongs to the archipelago of Puerto Rico and is located at ≈10.9°N 67.9°W, ≈70 km west of the main island. Mona Island is approximately 11 × 7 km, with a total surface area of ≈57 km^2 (Cintrón and Rogers 1991, Woodbury et al. 1976). Rainfall is strongly seasonal, averaging 810 mm per year, with an annual water deficit of the same magnitude (Woodbury et al. 1976). In Holdridge's life-zone system, the vegetation of the island is classified as subtropical dry forest (Cintrón and Rogers 1991, Ewel and

Whitmore 1973). Mona Island is a calcareous massif deposited on top of dolomite (Frank et al. 1998). The substrate has low water-retention capacity, and rainfall leaches easily after accumulating in cracks and crevices of variable depth. It was tectonically elevated and constitutes a platform with slight inclination to the south, from 80 m in the north to 20 m above sea level in the south. A variety of vegetation types are found on the island with height and density varying along the east–west axis, a pattern probably caused by the predominant northeasterly trade winds and associated salt-spray (Martinuzzi et al. 2008). The most extensive vegetation types are the ones covering the calcareous plateau and include deciduous forests, evergreen forests in depressions, shrublands, and cactus forests (Martinuzzi et al. 2008). Plants sampled for the present work included the most common and characteristic species of forests and shrublands as reported by Cintrón and Rogers (1991) and Woodbury et al. (1976).

Methods

Field teams from the Center for Applied Tropical Ecology and Conservation (CATEC; University of Puerto Rico-Río Piedras), the International Institute for Tropical Forestry (IITF; US Forest Service [USFS]), the USFS Southern Research Station Forest Inventory and Analysis (FIA) program, and the Department of Natural and Environmental Resources (DNER) of the Commonwealth of Puerto Rico sampled leaves of tree species identified in the field and present on a set of plots on Mona Island 17–22 November 2008, in conjunction with a survey of vegetation-cover data. A total of 37 plots were sampled following a modified version of the FIA plot design (USDA-FIA 2007). An FIA plot consists of a cluster of 4 circular subplots each with a radius of 7.3 m (1 central subplot with 3 subplots located 36.6 m away at azimuths of 120°, 240°, and 360°, respectively, from the center of the central subplot). For this study, field crews sampled trees from the 360° and 240° subplots for a total of 74 subplots across the island's plateau.

Crew members collected leaves of woody species as composite samples, usually from 2–3 individuals. The samples included fully expanded leaves at similar developmental stages representing the range of upper canopy leaves of each species at each plot. The number of samples per species was representative of the abundance and frequency of each taxon within the plots sampled. Collectors placed the leaves in paper bags and recorded the species, plot, and subplot identifiers on each sample bag.

We separated leaves and petioles from non-leaf materials (e.g., branches, flowers, or fruits) within 24–48 h after collection and discarded non-leaf or petiole material. Bags were left open to the air until samples were taken to the IITF lab for oven drying within 4 days. The high diurnal ambient temperature (>25 °C) and low humidity (<70%) prevented decomposition of leaf samples during this storage period.

We measured total N and C concentrations with a LECO True Spec CN element analyzer (LECO Consumables, St. Joseph, MI) and ash concentration with a Leco TGA701 at 490 °C.

We measured acid detergent fiber (ADF) and lignin concentrations using differential acid digestion originally designed by Goering and VanSoest (1970) and standardized by ANKOM (1998, 1999). Lignin was included within the % ADF; therefore we calculated the difference between % ADF and % lignin as the % c+h and used it instead of % ADF for statistical analyses.

We calculated descriptive statistics (mean, standard deviation, range, coefficient of variation, and degree of skewness and kurtosis) for each of the variables, and evaluated normality of distributions. We then tested for correlation among variables using Pearson correlation coefficients and a stepwise regression model to examine the sources of variation for leaf-C concentration. The set of species samples with complete analyses of C, N, ash, c+h, and lignin was evaluated using a clustering procedure (Ward method) to ascertain if species could be grouped based on the composition of their leaves and to determine the potential for variation within functional groups. We ran a principal component analysis (PCA) to quantify the spatial distribution of clusters along statistical axes. All statistical analyses were conducted using JMP 8 program (SAS 2008).

Results

Plant species

Field crews collected leaf samples from 53 species distributed among 31 families (Table 1). The most common families were: Rubiaceae and Euphorbiaceae (5 species each), Myrtaceae (4 species), and Polygonaceae and Rhamnaceae (3 species each). The most abundant species were *Coccoloba microstachya* (28 individuals); *Bursera simaruba* (27); *Croton glabellus* (20); *Stenostomum acutatum* (19); *Tabebuia heterophylla* (16); *Reynosia uncinata* (15); *Plumeria obtusa* (12); and *Croton discolor*, *Metopium toxiferum*, and *Myrcianthes fragrans* (10 each). These ten species were dominant in the plots sampled in this study, represent ≈19% of the species sampled, and contributed 167 leaf samples accounting for 59% of the total number of samples. Nineteen species were represented only by one sample (Fig. 1, Appendix 1).

Relationships between C, N, lignin, and c+h

The % C range was 27.1–58.5%, averaging 52.4% (Table 2); the lowest value corresponded to *Pilosocereus royenii*, due to the large accumulation of ash in this cactus. The rest of the species had C concentrations higher than 46%. Percent N averaged 1.40%; values were above 0.6%, except those of *P. royenii* (0.19%) and the large epiphyte *Tillandsia fasciculata* (0.22%). Ash % was exceptionally large in *P. royenii* (35.8%), and lowest in the epiphyte *T. fasciculata* (2.6%). Average ash was 8.8%. Lignin ranged from 1.5% in *Euphorbia petiolaris* to 34.0% in *Zizyphus taylorii*, averaging 14.3%. The % c+h ranged from 6.1% in *Exostema caribaeum* to 40.7% in *Megathyrsus maximus*, averaging 20.0% for the whole set of species. The molar C/N ratio varied widely from 25 in *Varronia bullata* to 102 in *Sideroxylon obovatum*; the outlier was the epiphyte *T. fasciculata* with a value of 277.

For the analysis of variable distributions, we excluded *Pilosocereus royenii* because of its extreme % ash value. In addition, the species *Bucida buceras*, *Varronia bullata*, *Malpighia setosa,* and *Tillandsia fasciculata* were not analyzed for % lignin and ADF because of sample loss. The distributions of the leaf parameter

Table 1. Species sampled by the International Institute for Tropical Forestry, Center for Applied Tropical Ecology and Conservation, and collaborators on Mona Island during 2008 in 37 plots. Names follows the list of Woodbury et al. (1976) and Cintrón and Rogers (1991) and were updated when necessary using Axelrod (2011) and the W^{3}Tropicos database of the Missouri Botanical Garden (www.tropicos.org).

Family	Species	Habit
Agavaceae	*Furcraea tuberosa* (Mill.) W.T. Aiton	Succulent rosette
Anacardiaceae	*Comocladia dodonea* (L.) Urb.	Small tree
	Metopium toxiferum (L.) Krug & Urb.	Tree
Apocynaceae	*Pentalinon luteum* (L.) B.F. Hansen & Wunderlin	Shrubby vine
	Plumeria obtusa L.	Shrub, small tree
Arecaceae	*Thrinax morrisii* H. Wendl.	Tree
Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	Tree
Boraginaceae	*Bourreria succulenta* Jacq.	Shrub, small tree
	Varronia bullata L.	Shrub
Bromeliaceae	*Tillandsia utriculata* L.	Epiphyte
Burseraceae	*Bursera simaruba* (L.) Sarg.	Tree
Cactaceae	*Pilosocereus royenii* (L.) Byles & G.D. Rowley	Arborescent
Canellaceae	*Canella winterana* (L.) Gaertn.	Shrub, small tree
Capparaceae	*Quadrella cynophallophora* (L.) Hutch.	Tree
Celastraceae	*Crossopetalum rhacoma* Cranz	Shrub
Combretaceae	*Bucida buceras* L.	Tree
Erythroxylaceae	*Erythroxylon aerolatum* L.	Tree
Euphorbiaceae	*Croton betulinus* Vahl	Shrub
	Croton discolor Willd.	Shrub
	Croton glabellus L.	Shrub
	Euphorbia petiolaris Sims	Shrub, small tree
	Gymnanthes lucida Sw.	Shrub, small tree
Fabaceae	*Chamaecrista nictitans* (L.) Moench	Shrub
Malphigiaceae	*Byrsonima lucida* (Mill.) DC.	Shrub
	Malpighia setosa Spreng.	Shrub
Malvaceae	*Corchorus hirsutus* L.	Shrub
	Helicteres jamaicensis Jacq.	Shrub
	Melochia tomentosa L.	Shrub
Meliaceae	*Swietenia mahagoni* (L.) Jacq.	Tree
Moraceae	*Ficus citrifolia* Mill.	Tree
Myrtaceae	*Calyptranthes pallens* Griseb.	Shrub, small tree
	Eugenia foetida Pers.	Shrub, small tree
	Eugenia monticola (Sw.) DC.	Shrub, small tree
	Myrcianthes fragrans (Sw.) McVaugh	Shrub, small tree
Nyctaginaceae	*Pisonia albida* (Heimerl) Britton & Standl.	Tree
Phyllanthaceae	*Phyllanthus epiphyllanthus* L.	Shrub
Poaceae	*Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs	Grass
Polygonaceae	*Coccoloba diversifolia* Jacq.	Shrub, small tree
	Coccoloba microstachya Willd.	Shrub, small tree
	Coccoloba uvifera (L.) L.	Shrub, small tree

values were normal except for % lignin (Table 2). The best fitting distribution, as measured by the Shapiro-Wilk W value, corresponded to % N and % C, followed by % c+h and % ash. The lack of normality in % lignin is probably related to the occurrence of sclerophyllous species with high lignin/C ratios (>0.35). Skewness of distributions was largest and positive for % lignin followed by % ash and % c+h and negative for % N, whereas kurtosis was negative for % C and % N but large and positive for % ash. The coefficient of variation was lowest for % C, intermediate for % N, % ash and % c+h, and large for % lignin (Table 2).

Table 1, continued.

Family	Species	Habit
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urb.	Tree
	Reynosia uncinata Urb.	Shrub, small tree
	Zizyphus taylorii (Britton) M.C. Johnst.	Shrub, tree
Rubiaceae	*Erithalis fruticosa* L.	Shrub
	Exostema caribaeum (Jacq.) Roem. & Schult.	Shrub, small tree
	Guettarda elliptica Sw.	Shrub, small tree
	Randia aculeata L.	Shrub
	Stenostomum acutatum DC.	Shrub, small tree
Rutaceae	*Amyris elemifera* L.	Shrub, tree
Sapindaceae	*Hypelate trifoliata* Sw.	Shrub, tree
Sapotaceae	*Sideroxylon obovatum* Lam.	Tree
	Sideroxylon salicifolium (L.) Lam.	Tree
Verbenaceae	*Lantana involucrata* L.	Shrub
Families:31	Species:53	

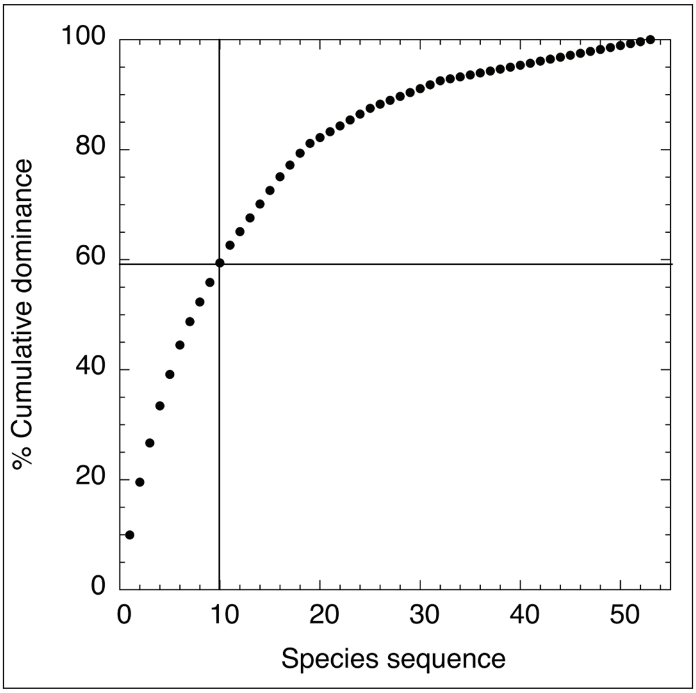

Figure 1. Cumulative dominance of the species set based on the number of samples as an approximation of the species abundance. The first 10 species are indicated in the text.

Pairwise correlations calculated using species averages ($n = 48$) were significant and negative between % C and % ash ($r = -0.76$, $P < 0.0001$), % N and % lignin ($r = -0.287$, $P = 0.048$), and % ash and % lignin ($r = -0.297$, $P = 0.041$), and positive for % C and % lignin ($r = 0.378$, $P = 0.008$). We obtained similar results when we calculated Spearman's non-parametric coefficients.

Species clustering and multivariate analysis

We identified four species clusters from the analysis output (Table 3). We conducted an analysis of variance of each of the properties of the groups identified in the cluster analysis. Cluster 1 was defined by its high % N and low % lignin. Clusters 2 and 4 showed low % ash, and cluster 4 had nearly twice as much fiber (% ADF). Cluster 3 had low % N and high %c+h, but the % lignin/% c+h ratio was about 0.5 (Table 3). Principal components analysis revealed that the first component was related to the % C–% ash axis and explained 40% of the variance, whereas the second component, determined by a % N–% c+h axis explained 27.5% of the variance (Table 4).

Discussion

The vegetation of Mona Island is mostly dominated by dry deciduous and semi-deciduous species that are adapted to conditions with low rainfall (≈800 mm) and high atmospheric evaporative demands (Woodbury et al. 1976). The first vegetation-cover study of Mona divided the island into 1) upland or plateau vegetation including forests, shrublands, cactus, and plate-rock communities, 2) depression forests, 3) coastal lowland vegetation including forests and shrublands, and 4) cliffside vegetation (Cintrón and Rogers 1991). A second vegetation study by Martinuzzi et al. (2008) used NDVI, derived from Landsat and Ikonos imagery, to detect 16 vegetation classes covering a total of 5556.78 ha. The vegetation-cover classes relevant for the present study were those located on the island's upland and were denominated, in order of decreasing size (ha), as dry limestone woodland (3207.96 ha), dry limestone semi-deciduous forest (875.61 ha), dry limestone shrubland (801.99 ha), and dry cactus forest and shrubland (46.71 ha). These classes

Table 2. Average and distribution of measured parameters for the species set of Table 1.

	% C	% N	% ash	% c+h	% lignin
n	53	53	53	49	49
Mean	52.4	1.4	8.8	20.0	14.3
Standard deviation	4.5	0.5	4.8	7.8	7.7
Range	27.1–58.5	0.2–2.3	2.6–35.8	6.1–40.7	1.5–34
Coefficient of variation	8.6	35.2	54.7	39.1	53.7
Distribution (excluding *Pilosocereus royenii*)	Normal	Normal	Normal	Normal	
Skewness	-0.09	-0.19	0.66	0.65	0.76
Kurtosis	-0.41	-0.26	0.43	0.17	-0.07
Shapiro-Wilk W	0.98	0.98	0.96	0.97	0.94
Probability < W	0.63	0.77	0.09	0.17	0.02*

account for 89% of the upland area. Woodbury et al. (1976) and Cintrón and Rogers (1991) list several characteristic or indicator species for each vegetation class (Table 5). *Coccoloba microstachya*, *Bursera simaruba*, *Tabebuia heterophylla*, and *Metopium toxiferum* are characteristic of the woody vegetation on the calcareous plateau, whereas *Quadrella cynophallophora*, *Coccoloba diversifolia*, *Ficus citrifolia*, *Pisonia albida*, and *Sideroxylon salicifolium* are typical trees of the forests in depressions. Characteristic species of shrublands include all the *Croton* species, *Stenostomum acutatum*, *Reynosia uncinata*, and *Plumeria obtusa*.

Table 3. Species groups separated using cluster analysis and averages of leaf components. Average numbers followed by the same letter within columns are not statistically different (Tukey-Kramer HSD test, $P = 0.05$). Number of species grouped = 49. Excluded for lack of fiber analysis: *Bucida buceras*, *Varronia bullata*, *Malpighia setosa*, and *Tillandsia fasciculata*.

Cluster number			
1	2	3	4
Amyris elemifera	*Bursera simaruba*	*Byrsonima lucida*	*Coccoloba microstachya*
Bourreria succulenta	*Calyptranthes pallens*	*Coccoloba diversifolia*	*Metopium toxiferum*
Corchorus hirsutus	*Canella winterana*	*Coccoloba uvifera*	*Phyllanthus epihyllanthus*
Croton discolor	*Chamaecrista nictitans*	*Crossopetalum rhacoma*	*Reynosia uncinata*
Croton betulinus	*Comocladia dodonaea*	*Eugenia monticola*	*Swietenia mahagoni*
Croton glabellus	*Erithalis fruticosa*	*Megathyrsus maximus*	*Thrinax morrisii*
Ficus citrifolia	*Erythroxylum aerolatum*	*Pisonia albida*	*Zizyphus taylorii*
Gymnanthes lucida	*Eugenia foetida*	*Sideroxylon obovatum*	
Helicteres jamaicensis	*Euphorbia petiolaris*	*Sideroxylon salicifolium*	
Lantana involucrata	*Exostema caribaeum*	*Quadrella cynophallophora*	
Melochia tomentosa	*Furcraea tuberosa*	*Tabebuia heterophylla*	
Pentalinon luteum	*Guettarda elliptica*		
	Hypelate trifoliata		
	Krugiodendron ferreum		
	Myrcianthes fragrans		
	Plumeria obtusa		
	Randia aculeata		
	Stenostomum acutatum		

Cluster number	% C	% N	% ash	% lignin	% c+h
1	50.95 b	1.87 a	9.7 a	7.9 c	20.6 a
2	55.23 a	1.40 b	6.8 b	14.1 b	14.5 b
3	50.59 b	1.05 c	10.3 a	14.3 b	26.2 a
4	54.75 a	1.38 bc	5.6 b	27.7 a	24.7 a

Table 4. Principal component analysis based on correlations.

Component	Eigenvalue	%	Cumulative %
1	2.01	40.0	40.3
2	1.37	27.5	67.6
3	0.93	17.7	86.3
4	0.52	11.4	96.6
5	0.10	73.3	100.0

The sets of species characteristic of each vegetation type partially conformed to the clusters of species identified by this study based on % C, % N, % ash, and % fiber content (see percentage of species clusters indicated for each vegetation type in Table 5). The upper canopy-tree component of forests on calcareous plateau habitat was dominated by cluster 2 species (medium % N and lignin), whereas in depression forests, it was characterized by species of cluster 3 (low % N, medium % lignin). The shrubby elements of the shrublands and lower canopy of calcareous

Table 5. Dominant species of forests and shrublands on the calcareous terrace of Mona Island, as described by Cintrón and Rogers (1991) with additional species from Woodbury et al. (1976) and equivalent community names from Martinuzzi et al. (2008) map. Names from Woodbury et al. (1976), updated following Axelrod (2011). * indicates species measured in this study. Cluster % corresponds to chemical groups for forests A and B, and shrubby + cactus vegetation (C + D)

Vegetation type	Canopy (>3 m)	Canopy (<3 m)	Cluster %
A. Forest on calcareous plateau	*Coccoloba microstachya**	*Croton discolor**	1) 22.2
(Dense deciduous forest	*Bursera simaruba**	*Croton humilis**	2) 44.4
and woodland)	*Tabebuia heterophylla**	*Croton betulinus**	3) 11.1
	*Plumeria obtusa**	*Stenostomum acutatum**	4) 22.2
	*Euphorbia petiolaris**	*Reynosia uncinata**	
	*Metopium toxiferum**		
B. Forest on depressions	*Quadrella cynophallophora**	*Euphorbia petiolaris**	1) 33.3
(Dense evergreen forest)	*Coccoloba diversifolia**	*Opuntia rubescens*	2) 41.6
	*Ficus citrifolia**	*Lantana involucrata**	3) 16.6
	*Krugiodendron ferreum**	*Phyllanthus epiphyllanthus**	4) 8.3
	*Myrcianthes fragrans**	*Reynosia uncinata**	
	*Pisonia albida**		
	Schaefferia frutescens		
	*Sideroxylon salicifolium**		
	Sideroxylon foetidissimum		
C. Shrubs on calcareous plateau		*Stenostomum acutatum**	1) 37.5
(Shrublands)		*Coccoloba microstachya**	2) 37.5
		*Croton discolor**	3) 12.5
		*Croton betulinus**	4) 12.5
		*Corchorus hirsutus**	
		*Crossopetalum rhacoma**	
		*Erithalis fruticosa**	
		*Euphorbia petiolaris**	
		*Melochia tomentosa**	
		*Pentalinon luteum**	
		*Plumeria obtusa**	
		*Randia aculeata**	
		*Reynosia uncinata**	
		*Tabebuia heterophylla**	
D. Cactus + shrubland vegetation			
(Dry cactus forest and	*Harrisia portoricensis*	*Corchorus hirsutus**	
shrublands)	*Pilosocereus royenii**	*Varronia bullata**	
	*Plumeria obtusa**	*Croton discolor**	
	Stenocereus hystrix	*Croton betulinus**	
	*Reynosia uncinata**		

plateau forests were dominated by species of clusters 1 and 2, characterized by total fiber contents (% ADF) above 28%). The species clusters reported here were associated with the ecophysiological properties of the species analyzed and probably site nutrient availability. Soil development in the upland plateau is limited (Woodbury et al. 1976). The underlying rock is calcareous and prone to erosion in the presence of water acidified with CO_2 from the atmosphere or contributed by root respiration and decomposition of organic matter in the litter layer (Lugo et al. 2001). The major nutrient sources in these areas are probably cations adsorbed by the clay accumulated in cracks and crevices, and deposited on the bottom of the depressions. It has been observed that woody vegetation is taller and denser in depression forests, likely as a result of higher water and, perhaps, also nutrient availability (see Woodbury et al. 1976:8).

Most species examined in this paper, except a cactus, an epiphytic bromeliad, a succulent rosette, and a grass, were woody and broad-leafed with a deciduous or semi-deciduous habit associated with seasonality of water availability. Leaf composition had a large range of variation that deserves more detailed analysis. The % C was comparatively high; 19 species showed values above 54%, well above the average usually found in plant leaves (≈45%, International Plant-Analytical Exchange 2013). Lal et al. (2001) analyzed tree species from tropical dry forests in India on different soil types. Deciduous species on ultisols had 45.4% C (n = 19) and those on inceptisols had 40.54% C (n = 35). Hättenschwiler et al. (2008) reported an average of 48.8% C for Amazonian evergreen species (n = 45). The carbon concentration of plant tissues is determined by the proportion of their organic components. Approximate carbon contents increase from around 44% in carbohydrates (starch, cellulose) to 53% in proteins (zein), 67% in lignin components (coniferyl alcohol), and 77% in typical lipids (glyceroltrioleate) (Vertregt and Penning de Vries 1987). Ash content also reduces the carbon concentration per unit dry weight.

The high % C values of the species on Mona Island are only partially explained by the concentration of lignin. Running a step-wise regression model using % C as the dependent variable and % c+h, lignin, and ash as the driving variables showed that the carbohydrate fraction explains only 7% of the variance, lignin 15%, and ash 60%. These three variables explain as much as 70% of the variance in C concentration in the samples of Mona Island leaves. Lipids are probably also in concentrations sufficiently high to explain the remaining variance fraction, a subject that deserves further investigation.

We found that % N was below 1% in two *Sideroxylon* species from depression forests, the succulent rosette of *Furcraea tuberosa*, the shrubs *Erithalis fruticosa* and *Eugenia monticola*, the grass *Megathyrsus maximus*, and the cactus *Pilosocereus royenii*. At the other extreme, 5 species had N concentrations above 2%, including the trees *Krugiodendron ferreum* and *Erythroxylon aerolatum*, mostly characteristic of depressions forests, and the shrubs *Croton betulinus, C. glabellus*, and *Chamaecrista nictitans* (the only legume in this species set). The other species varied between those limits, which are similar to the levels reported for other tropical dry forests (Lal et al. 2001), but lower than the range of values used by Kokaly et al. (2009) for deciduous forests (1–3.5%) or Hättenschwiler et al. (2008) for evergreen humid forests (1–2.6%). Nitrogen concentration in leaf tissues varies widely with leaf age and soil N availability (McGroddy et al. 2004). We assumed that sampled leaves were of similar age, because field crews collected only fully expanded leaves without obvious senescence symptoms (discoloration); presently, we have no information on nutrient availability from the actual substrate. We excluded the following two species from our N analyses: *Pilosocereus royenii* because of its succulent habit and *Tillandsia fasciculata* because its epiphytic habit leads to extremely low N concentrations. The mean molar C/N ratio we calculated for the present data set is 48 ± 18, much higher than the average of 35 quoted by McGroddy et al. (2004) for tropical forests and the range of 22–28 reported by Lal et al. (2001) for tropical dry forest species. This result may indicate a significant N limitation for the upland plateau vegetation in Mona Island, although the unusually high % C concentrations may have contributed to the increase in C/N ratios.

The average % cellulose of 21.47% (range = 12.4–33.4%) for deciduous forests obtained from the accelerated canopy chemistry program (Kokaly et al. 2009) is similar to the 19.5% (range = 1.7–41%) we calculated for our data set from the difference between % ADF and % lignin. The mean % c+h: % lignin ratio for the set of Mona species was 1.89 ± 1.47, very similar to 1.86 ± 0.52, as calculated for deciduous forests from the ACCP program by Kokaly et al. (2009), but the range in our data set is much wider. The few values available for cellulose content of wild grass species in ACCP are lower than that of the only grass species in our data set, but the % c+h:% lignin ratio is similar. On the other hand, % lignin (31%) and c+h (36%) reported for neotropical rainforest species (Hättenschwiler et al. 2008) are well above the averages we measured for Mona species.

Finally, we have observed that numerous species in our data set have characteristics often associated with herbivory deterrence: latex in *Plumeria obtusa, Euphorbia petiolaris, Metopium toxiferum, Pentalinon luteum*, and *Ficus citrifolia*; etheric oils in *Amyris elemifera, Lantana involucrata, Canella winterana, Eugenia foetida, Myrcianthes fragrans,* and *Gymnanthes lucida*; and trichomes in *Croton* spp., *Helicteres jamaicensis,* and *Melochia tomentosa*. It is possible that this high frequency of antiherbivore characteristics in the present flora of Mona Island is associated with grazing pressure exerted by *Capra aegagrus* Erxleben (Wild Goat) that survived introduction in the island during the 15th century.

We conclude that the leaf data analyzed here for a set of plant species including more than 90% of the common woody species that vegetate the calcareous plateau and associated depression forests constitute a useful background for interpretation of canopy spectra from remote-sensing devices.

Acknowledgments

This study was funded by NSF-CREST (HRD 0734826) through the Center for Applied Tropical Ecology and Conservation of the University of Puerto Rico. Additional funding, logistical help, and support for fieldwork in Mona Island were provided by the USDA Forest Service (USDAFS)-Forest Inventory and Analysis and the USDAFS-Southern Research

Station (T. Brandeis, D. Shipley, J. McCollum, and H. Marcano), IITF USDAFS (E. Helmer and I. Vicens), DNER (D. Cruz, S. Colón, M.T. Chardón, and H. López), and UPR (J. Fumero, A. Tolentino, and 36 volunteers). Staff of the chemistry laboratory at IITF-FS conducted the analyses of C and N. Two anonymous reviewers provided constructive criticisms that helped to improve the original version of this paper.

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Appendix 1. Full data set. Average concentrations of C, N, c+h, and lignin of leaves of woody plant species from Mona Island.

	C-N-Ash	% C		% N		% ash		Fiber	% c+h		% lignin	
Species	*n*	Mean	sd	Mean	sd	Mean	sd	*n*	Mean	sd	Mean	sd
1. *Amyris elemifera*	6	52.00	1.76	1.95	0.14	10.18	1.25	6	16.73	1.71	9.39	1.04
2. *Bourreria succulenta*	9	52.41	1.79	1.65	0.19	10.97	0.62	9	22.73	3.18	8.16	2.82
3. *Bucida buceras*	1	54.99	.	1.05	.	4.73	.					
4. *Bursera simaruba*	27	54.64	2.12	1.44	0.17	8.09	1.46	25	18.11	2.11	19.29	3.89
5. *Byrsonima lucida*	1	54.89	.	1.17	.	5.82	.	1	35.95	.	10.45	.
6. *Calyptranthes pallens*	1	57.78	.	1.12	.	4.05	.	1	18.52	.	19.08	.
7. *Canella winterana*	3	54.52	2.88	1.54	0.07	10.39	2.06	3	10.39	0.44	11.84	0.30
8. *Chamaecrista nictitans*	7	58.26	1.20	2.24	0.29	4.54	1.09	5	14.05	3.41	15.25	3.17
9. *Coccoloba diversifolia*	3	50.76	1.80	1.27	0.37	10.64	0.68	3	24.78	2.51	25.62	1.41
10. *Coccoloba microstachya*	28	54.19	1.59	1.23	0.20	5.29	0.69	27	30.79	4.13	30.21	4.48
11. *Coccoloba uvifera*	1	49.19	.	1.05	.	10.36	.	1	26.11	.	18.79	.
12. *Comocladia dodonaea*	7	54.67	1.05	1.54	0.25	5.60	0.94	6	19.64	3.60	9.06	1.72
13. *Corchorus hirsutus*	5	51.38	1.19	1.88	0.28	8.10	1.71	4	24.86	0.49	5.99	1.45
14. *Crossopetalum rhacoma*	1	51.39	.	1.16	.	10.15	.	1	26.74	.	13.26	.
15. *Croton betulinus*	3	52.21	1.58	2.19	0.18	9.12	0.86	2	19.68	3.60	8.97	0.79
16. *Croton discolor*	10	50.70	2.27	1.85	0.34	8.46	1.63	10	31.63	3.30	6.46	0.75
17. *Croton glabellus*	20	51.64	1.87	2.13	0.23	10.80	1.39	17	12.33	1.97	9.13	3.82
18. *Erithalis fruticosa*	2	55.25	1.42	0.79	0.06	7.68	1.20	2	7.94	0.10	16.71	4.41
19. *Erythroxylum aerolatum*	1	57.62	.	2.05	.	5.50	.	1	16.41	.	9.79	.
20. *Eugenia foetida*	7	55.66	0.97	1.31	0.17	6.08	0.84	6	13.59	1.57	21.73	2.05
21. *Eugenia monticola*	1	50.62	.	0.86	.	8.78	.	1	36.16	.	16.24	.
22. *Euphorbia petiolaris*	7	53.01	2.20	1.68	0.20	5.47	0.91	3	10.20	1.45	1.47	0.27
23. *Exostema caribaeum*	3	54.35	1.22	1.55	0.22	5.23	0.40	3	6.07	0.88	6.17	2.18
24. *Ficus citrifolia*	1	50.50	.	1.82	.	11.39	.	1	18.04	.	9.86	.
25. *Furcraea tuberosa*	1	51.90	.	0.63	.	7.86	.	1	12.72	.	11.28	.
26. *Guettarda elliptica*	6	54.87	0.75	1.15	0.08	6.01	0.60	6	19.74	2.77	11.17	3.26

Species	C-N-Ash	% C		% N		% ash		Fiber	% c+h		% lignin	
	n	Mean	sd	Mean	sd	Mean	sd	*n*	Mean	sd	Mean	sd
27. *Gymnanthes lucida*	1	48.94	.	1.96	.	9.86	.	1	20.70	.	5.10	.
28. *Helicteres jamaicensis*	1	52.61	.	1.77	.	8.59	.	1	32.93	.	6.07	.
29. *Hypelate trifoliata*	2	52.93	0.97	1.20	0.13	11.10	2.98	2	13.89	4.43	14.82	3.91
30. *Krugiodendron ferreum*	2	55.33	1.32	2.04	0.20	8.50	1.06	2	13.15	0.81	24.15	3.92
31. *Lantana involucrata*	2	51.19	3.70	1.88	0.01	10.31	4.79	2	15.70	1.77	4.80	1.63
32. *Malpighia setosa*	1	50.40	.	1.53	.	9.37	.					
33. *Megathyrsus maximus*	1	49.89	.	0.71	.	7.23	.	1	40.66	.	7.24	.
34. *Melochia tomentosa*	1	49.29	.	1.88	.	8.47	.	1	18.99	.	8.31	.
35. *Metopium toxiferum*	10	56.21	1.81	1.49	0.22	6.22	1.07	10	19.96	1.86	29.45	3.12
36. *Myrcianthes fragrans*	10	53.80	0.93	0.99	0.13	7.72	1.02	10	17.42	2.12	11.31	2.25
37. *Pentalinon luteum*	1	48.57	.	1.48	.	10.06	.	1	13.46	.	12.44	.
38. *Phyllanthus epiphyllanthus*	7	52.97	1.35	1.35	0.17	6.57	1.09	8	27.71	3.54	26.58	6.42
39. *Pilosocereus royenii*	1	27.06	.	0.19	.	35.76	.	1	7.35	.	3.75	.
40. *Pisonia albida*	3	49.22	3.18	1.28	0.54	12.98	2.10	3	20.24	5.21	10.20	4.22
41. *Plumeria obtusa*	12	57.49	1.31	1.67	0.20	6.85	1.22	12	10.72	1.15	16.76	2.88
42. *Quadrella cynophallophora*	2	46.20	1.63	1.45	0.37	14.84	1.53	2	18.70	2.02	11.56	3.36
43. *Randia aculeata*	3	55.61	1.78	1.17	0.13	6.48	1.25	3	14.61	1.06	17.76	2.68
44. *Reynosia uncinata*	15	53.72	1.47	1.24	0.15	5.74	0.76	15	28.00	1.60	26.13	2.88
45. *Sideroxylon obovatum*	1	50.92	.	0.59	.	13.78	.	1	18.24	.	16.66	.
46. *Sideroxylon salicifolium*	2	51.39	2.79	0.67	0.16	12.66	0.65	2	17.21	0.38	14.69	3.15
47 *Stenostomum acutatum*	19	56.43	1.68	1.06	0.08	5.64	0.65	19	23.42	2.64	15.72	6.29
48. *Swietenia mahagoni*	2	58.52	0.31	1.26	0.25	4.43	0.15	2	17.10	0.59	28.61	7.19
49. *Tabebuia heterophylla*	16	50.79	1.49	1.26	0.17	10.56	1.52	16	24.24	2.35	12.68	2.14
50. *Thrinax morrisii*	1	54.25	.	1.78	.	5.22	.	1	28.28	.	18.82	.
51. *Tillandsia fasciculata*	1	51.78	.	0.22	.	2.59	.					
52. *Varronia bullata*	1	50.68	.	2.32	.	17.27	.					
53. *Zizyphus taylorii*	1	53.41	.	1.34	.	5.68	.	1	21.12	.	33.98	.