Caribbean Journal of Science, Vol. 46, No. 2-3, 203-215, 2010

Structural variability and species diversity of a dwarf Caribbean dry forest

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REVISED VERSION: APRIL 25, 2010

Abstract.—Low stature woody vegetation of the south-west coast of Puerto Rico grows on a rocky calcareous substrate where plants can only root in holes, cracks, and crevices accumulating water and sediments that allow seed germination and seedling development. Being in a coastal location these communities are influenced by steady onshore winds, high solar radiation, and salt spray. We studied dwarfed forest communities located at the southern limit of the Guánica State Forest, Puerto Rico, that have a well known floristic composition, but with little information on their organization and heterogeneity. We quantified the species composition of vegetation plots located along the southern coastline and compared their structure and diversity with those of dry forests on neighboring hills. The hypothesis was that forest structural development was negatively associated with proximity to the coast line and altitude above sea level. Species richness of the coastal dwarf forest area was similar to that of inland semi deciduous forest plots with which it shares at least 15 woody species. In addition, it contains a number of species resistant to salt spray and possibly brackish water, such as *Conocarpus erectus*, *Strumpfia maritima*, and *Coccoloba uvifera*. The average canopy height of the coastal vegetation increases from 0.4 to 2.3 m between 0 to 150 m from the coastline and 7 to 19 m elevation above sea level. Within this spatial range the predominant bearing of the canopy changes from a SE-NW direction to a SW-NE direction revealing the influence of onshore winds in combination with salt spray. The dominant woody species occur as multistemmed individuals, a characteristic probably associated to occasional heavy winds and recurrent drought that impairs shoot apical dominance. Floristic and structure comparisons with mature forest plots located between 25 and 150 m altitude showed that the coastal dwarf vegetation has a more even species dominance distribution associated with the discontinuity of substrate available for establishment.

Keywords.—coastal dry forests, community structure, species diversity, importance value, limestone substrate, multistemmed trees, plasticity, species dominance

Introduction

Dry coastal forests on calcareous substrate in the Caribbean present different physiognomies according to soil depth, slope, and distance from the coastline (Borhidi 1993). In the Guánica Dry Forest Biosphere reserve (Guánica Forest), in southwest Puerto Rico, Lugo et al. (1978) distinguished three community types not affected by salt or disturbed by human influences: a thorn forest with cacti and rock outcrops, a deciduous forest, and a semi-evergreen forest. In the same area, using Landsat ETM imagery, Gould et al. (2008) distinguished seven physiognomic lowland dry limestone types: woodland and shrubland, dry cactus shrubland, cliffside semi-deciduous forest, shrubland, woodland, and finally a coastal dry woodland and shrubland (CDWS). In those forests, floristic composition and community structure varies according to exposure slope in a fashion apparently related to water availability and soil depth (Murphy et al. 1995, Van Bloem 2004, Molina and Lugo 2006, Agosto Díaz 2008).

Soil development on these sites is scanty, plants root in holes formed by dissolution of the calcareous substrate, or in cracks and crevices breaking through the calcareous plaque, where mineral and organic residues accumulate. Permanence of established plants is affected by the consequent environmental harshness. Both water and nutrients are limited by shallow soils on the calcareous substrate. In addition, strong south-easterly winds blowing during the summer season affect shoot development through mechanical and drought stresses. These winds may also transport salt spray that further impairs shoot development.

Under these ecological constraints we expect to find a highly heterogeneous vegetation distribution, with a tendency towards species dominance in small plots that varies as the surveyed area increases as a result of random availability of appropriate sites regulating plant establishment.

Several structural studies of plots at different locations in the main area of the Guánica forest have been carried out, most of them at elevations around 100 m above sea level (Lugo et al. 1978, Murphy and Lugo 1986, Molina and Lugo 2006, Van Bloem 2003, 2005). Recently Agosto Díaz (2008) undertook a large scale structural analysis of the Guánica forest reserve that included plots in the area studied in this paper. Those studies support the assumption that structural development of woody plant communities is related to the distance from the sea, soil depth, and wind shearing.

Our objective was to characterize the structure and floristic composition of the coastal south eastern border of the Guánica forest reserve, covered by a dwarfed vegetation mostly less than 1.5 m tall, and containing numerous tree species that also grow in the medium (2-3 m) and tall (3-9 m) dry forests in areas located above 50 m elevation.

Methods

The study was carried out within the Guánica Forest (Unesco Biosphere Reserve) in southwest Puerto Rico. We quantified floristic and structural features of the vegetation near sea level in a band approximately 400 x 700 m located parallel to the coast (Fig. 1). We identified the area as a dwarf coastal forest that corresponds to the Coastal Dwarf Woodland and Shrubland on rocky limestone substrate (CDWS) described from satellite imagery by Gould et al. (2008). In this area we established 13 circular plots of 5 m radius (78.4 m^2), avoiding large vegetation-free rocky outcrops. As there was a rapid change in elevation and vegetation density perpendicularly from the coast line, plots were established south and north of the dirt path shown in Fig. 1, running approximately parallel to the coast line. The position of the plots was recorded using a Garmin Geographic Positioning System. At each plot we counted the number of stems of all woody species, and measured height and crown area of each individual tree. As crowns were not circular we measured the longest axis, and the axis perpendicular to it. Crown area was calculated assuming that they had nearly elliptical shapes as $[(D_1/2) * (D_2/2)] * \pi$. Importance Value indices were calculated following Mueller-Dombois and Ellenberg (1974), but using crown area instead of basal area as a dominance value (IVI = [relative frequency + relative density + relative dominance]/3). For interplot comparison we used an importance value per species calculated as one half of the sum of relative density and crown area.

In addition, we measured the bearing of the longest crown axis of each individual using a compass. To estimate the species/area relationship the plots were arranged in a random sequence and then the cumulative number of species per plot were plotted against cumulative area.

Plots comparisons were performed using a simple similarity index (Sørensens index, Magurran 2004) based on species presence assuming an arbitrary value of 0.5 to separate groups of plots. In addition, we conducted multivariate analyses (correlation and cluster analyses) (JMP 2008) based

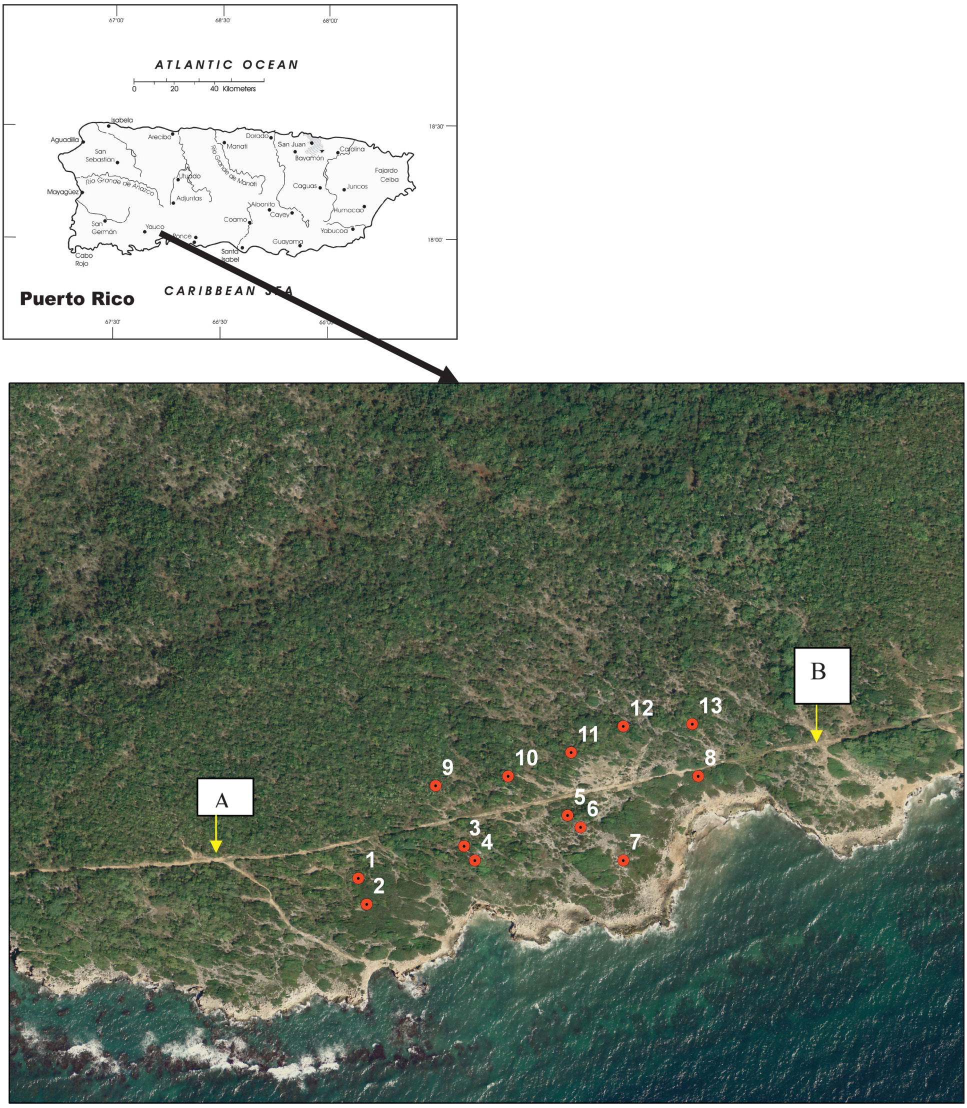


FIG. 1. Location of the Guánica Forest reserve and satellite image (Recursos Naturales 2006) indicating the sampling plots reported in the present paper. Distance A-B= 508 m. Locations A: (10 m asl) 17.95094 N; 66.83937 W (WGS 1984) B: (6 m asl) 17.9574 N; 66.83466 W

on species importance values (density + cover) for interplot comparisons, and based on IVI for comparing the dwarf coastal forest with other studies conducted in other sites within the Guánica Forest.

RESULTS

1. Vegetation cover

We found 468 individuals distributed among 41 species (Table 1). There was a tendency for species dominance, but degree of dominance and species composition varied among plots. Of the total canopy area, 13.2 % corresponded to 30 individuals of *Pisonia albida*, whereas 12.8 % belonged to *Conocarpus erectus* with only 5 individuals. The average height (mean ± sd) of the vegetation was 1.41 ± 0.59 m. Regarding the number of individuals the shrub *Erithalis fruticosa* dominated the area with more than 80 individuals/0.1 ha. The relative

TABLE 1. Floristic and structural properties of 13 plots (78.7 m^2 ea., total area: 1021 m^2) on the coastal border of the Guánica Forest. Plant names following Liogier (1985-1997). T:tree; S:shrub

SPECIES	Life Form	Fruit	N°Ind.	Av.Ht. m	Crown m^2	% IVI
Pisonia albida	T	Anthocarp	30	1.62	136.7	7.47
Erithalis fruticosa	S-T	Drupe	81	1.36	69.2	7.22
Reynosia uncinata	S-T	Drupe	36	0.87	70.9	7.08
Croton rigidus	S	Capsule	29	0.73	36.7	6.71
Antirhea acutata	S-T	Drupe	20	1.04	37.2	5.37
Coccoloba microstachya	S-T	Drupe	24	1.89	66.0	5.06
Erythroxylum areolatum	T-S	Drupe	15	1.53	47.0	4.77
Pilosocereus royenii	Col. Cacti	Berry	19	1.96	22.9	4.65
Comocladia dodonaea	T-S	Drupe	13	1.57	22.6	4.55
Eugenia foetida	S-T	Berry	41	1.70	16.5	4.37
Guettarda krugii	S-T	Drupe	17	1.58	34.2	2.92
Strumpfia maritima	S	Drupe	29	0.44	40.5	2.57
Jacquinia armillaris	T-S	Berry	8	1.85	5.3	2.55
Melochia tomentosa	S	Capsule	5	0.29	8.3	2.53
Conocarpus erectus	T-S	Cone	5	0.55	132.7	2.27
Lantana involucrata	S	Drupe	9	1.12	11.0	2.02
Colubrina arborescens	T-S	Capsule	6	1.59	14.2	1.99
Eugenia rhombea	S-T	Berry	5	1.40	9.7	1.94
Crossopetalum rhacoma	S-T	Drupe	6	0.87	1.9	1.90
Bourreria virgata	S-T	Drupe	4	1.11	4.9	1.89
Tabebuia heterophylla	T	Silique	7	1.38	54.7	1.72
Coccoloba krugii	S-T	Drupe	10	1.86	45.9	1.70
Thrinax morissii	Palm	Capsule	12	1.82	22.9	1.56
Ficus citrifolia	T-S	Syconium	3	0.63	34.6	1.50
Amyris elemifera	S-T	Drupe	3	1.75	6.9	1.29
Bursera simaruba	T	Capsule	2	2.10	6.6	1.27
Capparis indica	T-S	Berry	3	2.00	3.8	1.27
Plumeria alba	S-T	Follicle	3	2.20	0.1	1.24
Coccoloba diversifolia	T	Drupe	5	1.43	14.7	0.79
Unknown species	T		1	2.30	23.6	0.79
Coccoloba uvifera	T	Drupe	2	1.01	15.8	0.75
Randia aculeata	S-T	Berry	6	0.73	1.1	0.70
Coccoloba costata	S-T	Drupe	1	1.65	3.3	0.64
Krugiodendron ferreum	T-S	Drupe	1	1.35	3.3	0.64
Guettarda ovalifolia	T	Drupe	1	1.56	2.2	0.63
Bumelia krugii	S-T	Berry	1	2.13	1.3	0.62
Gymnanthes lucida	T-S	Capsule	1	1.09	1.0	0.62
Eugenia cf cordata	S-T	Berry	1	0.36	0.8	0.62
Bourreria succulenta	S-T	Drupe	1	0.59	0.7	0.62
Forestiera segregata	S-T	Drupe	1	2.81	0.6	0.62
Guaiacum officinale	T	Capsule	1	1.80	0.5	0.62
41 species			468	1.41(±0.59)	1033	100

IVI was regularly distributed showing a declining logarithmic pattern in which 9 species contributed around 50% of total IVI, whereas the 13 least important species contributed less than 9% of total IVI. The species-area curve obtained by fitting a 2nd degree polynomial approaches saturation between 900 and 1000 m^2 (Fig. 2).

The species list in Table 1 is characterized by the predominance of woody species recorded as trees or shrubs in different environments (Liogier 1985-1997). Definition of shrubby and tree life forms in the context of our study may be controversial. Shrubs are woody life forms branching from the base of the individual,

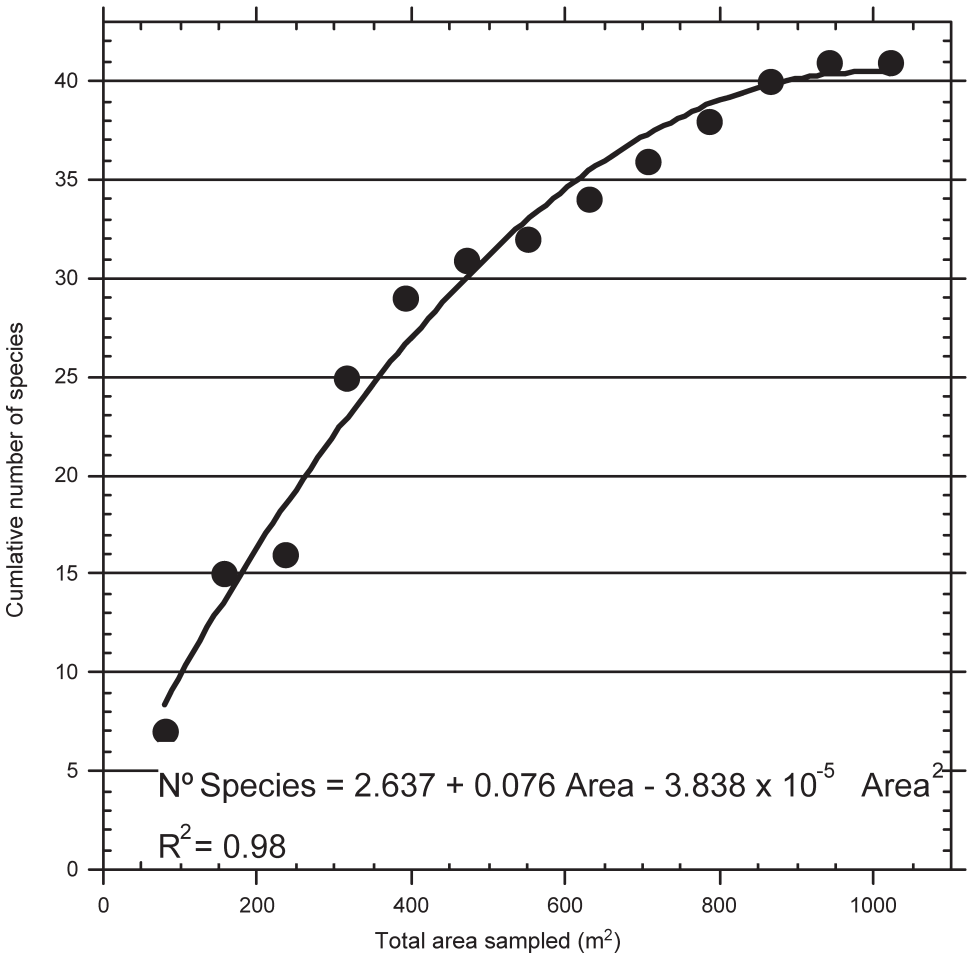


FIG. 2. Species/Area curve for the dwarfed coastal vegetation. The random sequence of plots was fitted to a 2nd order polynomial.

whereas trees are considered woody plants forming a distinct stem. Some confusion may arise when applied to a plant community where multistemmed species occur (see below). We consider the variation between shrubby and tree habit within a species as an indication of morphological plasticity enabling it to adjust to water and nutrient demands according to the environmental conditions. From the 41 species listed in Table 1, 8 are considered trees (T), 4 are strictly shrubs (S), 9 occur as trees or shrubs (T-S), 18 occur as shrubs or small trees (S-T) depending on environmental conditions. Columnar cacti do not comply to this classification.

Another remarkable aspect of this vegetation is the predominance of species with fleshy fruits (drupes and berries), most probably being dispersed by animals. The most important species, *P. albida,* produces achenes covered by persistent calyces with glandular hairs that attach effectively to many surfaces. This species is dispersed by passing animals, particularly birds. *Tabebuia heterophylla* is the only wind dispersed species recorded in our inventory.

The trees frequently presented dwarfed or gnarled habits apparently related to wind shearing, but this tendency decreased with the distance from the coastline. Exceptions from this general pattern were

Jacquinia armillaris, *Thrinax morrisii* and *Pilosocereus royenii*.

A common structural feature in the plots was the occurrence of multiple stems. This was observed in most individuals of *E. fruticosa*, *C. microstachya*, *C. diversifolia*, *R. uncinata*, *P. albida*, *E. foetida* and *C. arborescens*. The causes of this feature are mainly associated with the effect of strong winds and will not be further analyzed here (see Dunphy et al. 2000).

2. Plot heterogeneity

The pair of dominant species (covering together more than 30% of total plot crown area) varied among plots (Table 2). The number of dominant and subdominant species pairs per plot was the same as the number of plots. *Pisonia albida* was dominant or subdominant in 5 out of the 13 plots, whereas the rest dominated only in 1 or 2 plots.

This high variability may be caused by too small plots, by the confluence of different phytosociological units, a high level of environmental stress (salt spray, availability of soil sites, wind shearing) or physical disturbance (fire, herbivory, wood cutting). As we did not find evidences of recent anthropogenic disturbances we analyzed in more detail the structure and location of the plots.

Sørensens similarity index (k≥0.5) separated plots 1,2,9, and 12 from 3, 4, 5, 10, and 11. Plots 6, 7, 8, and 13 showed similarity indexes below 0.5 with any of the other plots. However, Sørensens index is highly sensitive to small samples, particularly with incidence of rare species (Chao et al. 2005). The cluster analysis using species importance values, that takes into consideration both species cover and density, provided a better plot classification. Absent species in a given plot were assigned the value 0. The analysis detected two clearly defined groups, one constituted by plots 1, 2, 11, 12, 9, and 3, and a second constituted by plots 4 to 8 (Fig. 3). The separation is due mainly to the occurrence in the second group of *C. uvifera*, *C. erectus*, and *S. maritima*, that are halophytes or salt spray tolerant species. Plots 13 was separated from the rest probably because of the presence of unique tree species.

The height distribution per plot suggested that plot location was correlated with plant height (Fig. 4). The same pattern was observed with medians and geometric means. Plots 9 to 13 located farther from the coast at slightly higher elevations showed heights above average, whereas the plots 4 to 8, nearest to the coastline, had heights well below average. Plot 1 to 3 occupied an intermediate position.

3. Crown orientation

The vegetation nearest to the coastline (plots 1 to 8) had their crowns oriented

TABLE 2. Crown dominance and variation in species dominance in the Coastal Dry Woodland and Shrubland plots.

PLOT	Dominant Species	% Crown	Subdominant Species	% Crown	N° Spp.
1	*Erithalis fruticosa*	42	*Coccoloba microstachya*	37	12
2	*Pisonia albida*	41	*Coccoloba diversifolia*	22	10
3	*Pisonia albida*	42	*Antirrhea acutata*	13	11
4	*Ficus citrifolia*	31	*Reynosia uncinata*	31	10
5	*Tabebuia heterophylla*	62	*Strumpfia maritima*	25	11
6	*Strumpfia maritima*	29	*Ficus citrifolia*	20	8
7	*Conocarpus erectus*	59	*Croton rigidus*	14	7
8	*Conocarpus erectus*	82	*Coccoloba uvifera*	18	2
9	*Pisonia albida*	16	*Coccoloba krugii*	16	14
10	*Reynosia uncinata*	44	*Erythroxylon areolatum*	24	13
11	*Erithalis fruticosa*	36	*Pisonia albida*	24	11
12	*Coccoloba microstachya*	19	*Pisonia albida*	17	12
13	*Coccoloba krugii*	28	Unidentified	19	14

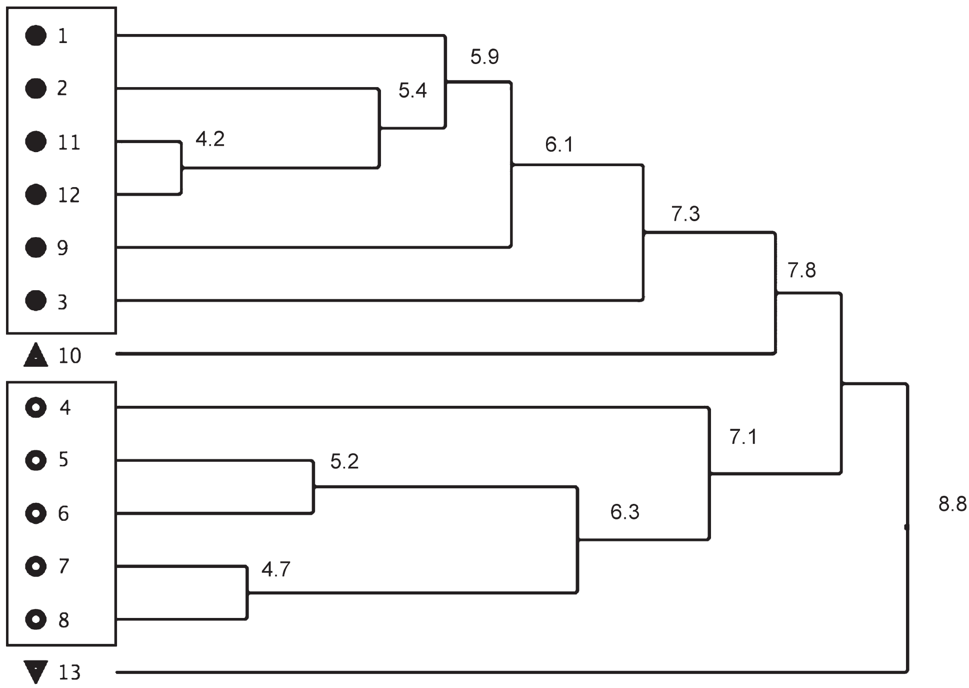


FIG. 3. Cluster analysis of the dwarf forest plots based on relative importance values (% density + % cover) using the Ward's minimum variance method (JMP 2008). Numbers on the joiners indicate distance between groups.

along a south-east to north-west direction, whereas in the vegetation further inland and at higher elevation (plots 9 to13) this orientation was not so obvious. Using the bearing of the longest crown axis we calculated the number of crowns falling within specific quadrants. For the graphic representation we added up the complementary angles (to all angles < than 180° we added 180°). The distribution of orientation angles showed that the plots 1 to 8 had predominantly an orientation SE to NW (115° to 295°), whereas the taller vegetation in plots 9 to 13 had predominantly a SW to NE orientation (236° to 56°) (Fig. 5).

Discussion

There are several descriptions of the floristic, physiognomic, and landscape aspects of coastal scrub vegetation in the Caribbean islands (see Borhidi 1993, Areces-Mallea et al. 1999, Helmer et al. 2002, Gould et al. 2008). Danserau (1966) described in Puerto Rico several types of coastal vegetation as scrubs within his "littoral subzone, supratidal belt" with rocky limestone pavement. The Danserau's vegetation units more similar in species composition to the Guánica dwarf coastal forest described here are the "sea-grape" scrub (Type N° 20.4) dominated by *C. uvifera*, the "snake-bark" scrub dominated by species of *Colubrina, Amyris, Comocladia, Reynosia* and *Oplonia* (Type N° 22.4) and the "roble prieto" scrub dominated by species of *Tabebuia, Randia, Plumeria,* and *Elaeodendron*.

Woodbury et al. (1977) published a detailed description of the coastal dwarf woody vegetation on calcareous substrates in Mona Island. The authors described it as "... a very dwarfed vegetation due to the strong winds, salt spray and the meager soil deposits...". These areas were also identified in the field by Cintrón and Rogers (1991) and detected by Martinuzzi et al. (2008) using remote sensing techniques. The dwarf woody vegetation of Mona Island included several genera and species characteristic of our Guánica Forest site, such

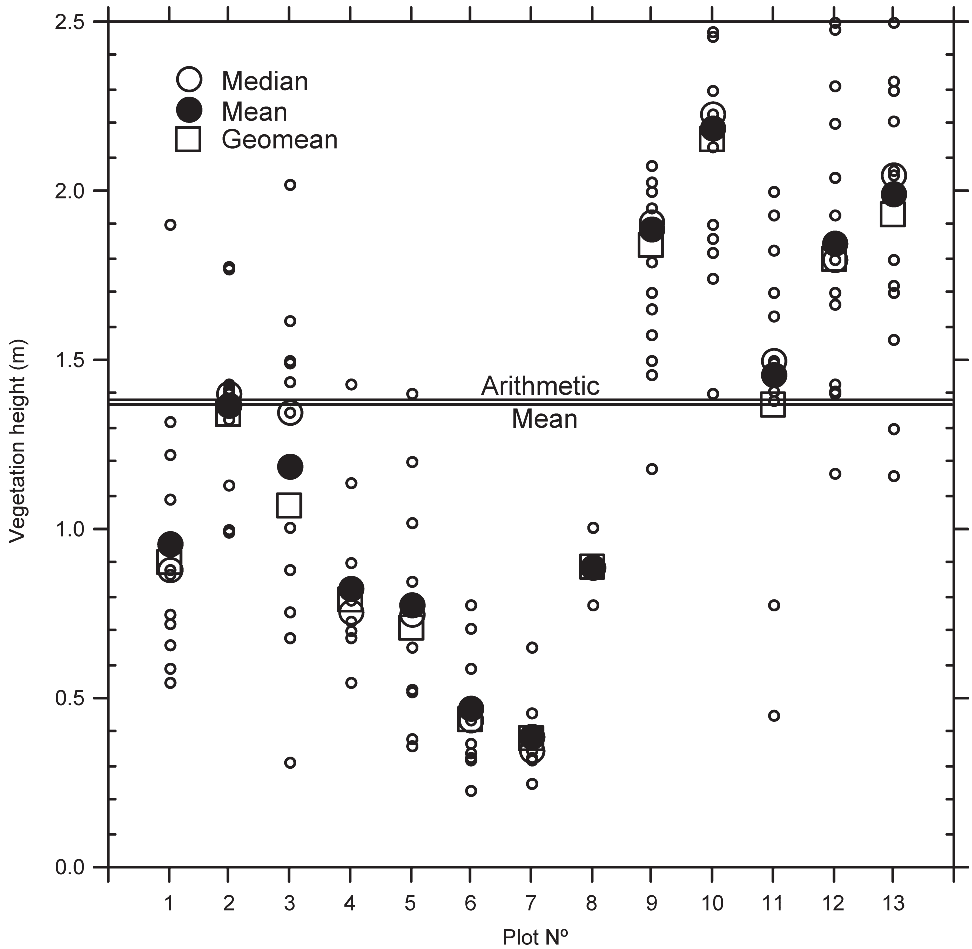


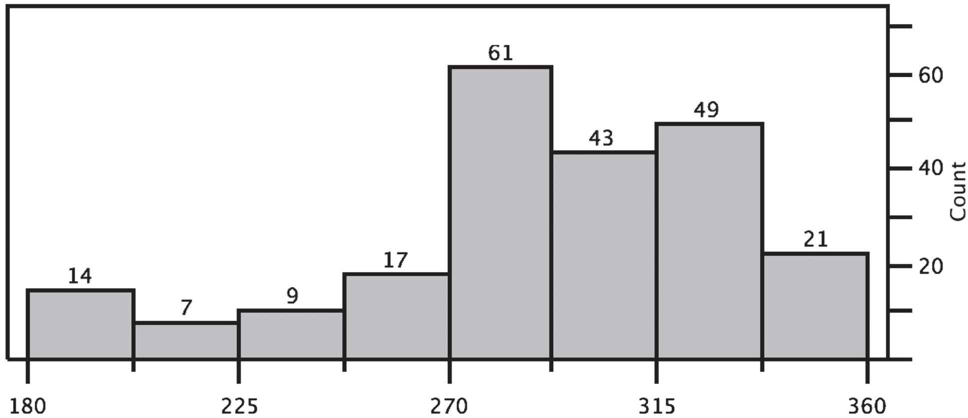
FIG. 4. Average crown height of all individuals per species in each vegetation plot (open dots). As normality of height distribution within plots was not tested the values of median, mean and geomean were also plotted.

as *Pilosocereus royenii*, *E. fruticosa*, *A. acutata*, *R. uncinata*, *T. heterophylla*, *R. aculeata*, *M. tomentosa*, and *C. rhacoma*.

Considering the convergence in physiognomy and species composition of these coastal sites, the question arises if the dwarfed vegetation should be considered a different phytosociological unit, or simply derives from the dry forests growing on the ridges and slopes of the Guánica Forest, as an expression of the environmental constraints prevailing in this coastal environment. To answer this question we compared our results with floristic and structural analyses conducted in upland mature forests elsewhere within Guánica Forest (Lugo et al. 1978, Murphy and Lugo 1986, Molina 1998, Van Bloem 2004). We are aware that those mature forests may have been disturbed by humans in the not so distant past (Molina Colon and Lugo 2006; Agosto Díaz 2008), but we assume that they have attained an advanced successional state that makes them representative stands of the original forests. Incidence of hurricanes in the area have certainly had severe effects inducing stand renovation and multistemmed trees, but the general structure and stand composition appears stable (Van Bloem et al. 2003).

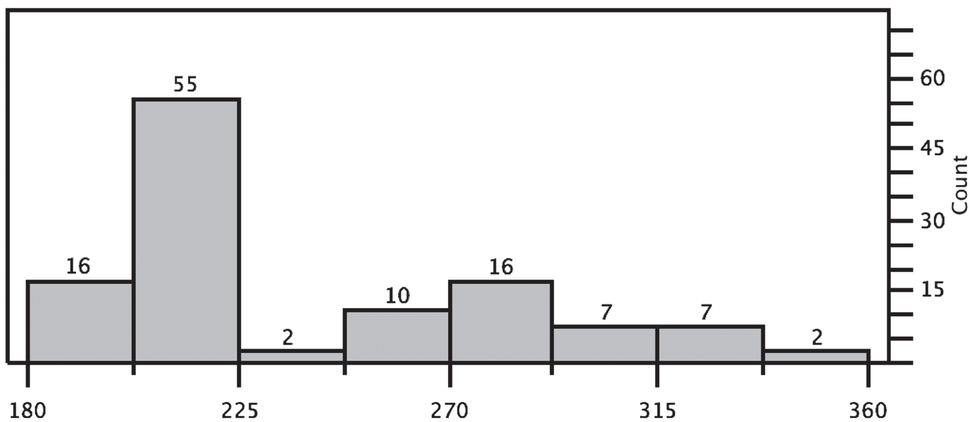
Murphy and Lugo (1986) reported 33 species with diameters ≥2.5 cm in fifteen 10 x 10 m plots in relatively undisturbed forest sites located on the Guánica Forest ridge. In this area (1500 m^2) the number of

Plots 1 to 8



Mean ±sd 295 ± 42; N=237
Upper 95% Mean 301; Lower 95% Mean 290
Skewness -0.686; Kurtosis 0.122

Plots 9 to 13



Mean ± sd 236±44; N 115
Upper 95% Mean 244; Lower 95% Mean 228
Skewness 0.739; Kurtosis -0.748

FIG. 5. Distribution of bearings of the longest crown axes measured in plots 1 to 8 and 9 to 13. Bearings were aded to fall into the 180 to 360 quadrants.

species with diameters between 2.5-4.99 cm leveled off at 275 m^2 and for trees ≥ 5 cm in dbh the leveling off area was 1200 m^2. Molina (1998) measured structural properties of mature forest patches on the northern slope of Guánica Forest setting 5 circular plots of 400 m^2, and found 37 tree species ≥ 2.5 cm DBH in the 2000 m^2 surveyed. She also calculated a similar minimum area for trees within the same DBH range.

Our study yielded similar numbers as the species/area curve just begins to level off at 1000 m^2, but the number of woody species recorded within 1020 m^2 was 41, slightly larger than the number reported for larger areas of mature forest. However, our study included all species with woody stems present in the plots.

Van Bloem (2004) remeasured Murphy and Lugo (1986) plots and concluded that this forest site was in a stable structural condition associated with similar mortality and in-growth values. Assessment of forest structure in two other places by Van Bloem (2004) (Lluberas and Ventana) revealed that the number of tree species found in 900 m^2 areas ranged from 31 to 34, and variations in stem density (6,400 to 10,400) were more pronounced than associated changes in basal area (17.9 to 21.3 m^2 ha^{-1}). Our plots had lower densities, 4000 to 5000 stems/ha, but the number of species was slightly larger probably because smaller sized DBH classes were included.

The Guánica sites compared here show a relatively high degree of similarity in species composition (Sørensen's index >0.5, data not shown). This is partially explained by the fact that a group of 15 tree species are shared by all vegetation units. The most important are *B. buceras*, *B. simaruba*, *C. diversifolia*, *C. arborescens*, *E. areolatum*, *G. lucida*, *P. albida*, and *T. heterophylla*. However, sites differed in the pair of dominant-subdominant species (Table 3). The Northern Slope site was dominated by the pair *C. diversifolia-B. buceras*, the sites at the Ridge, Lluberas and Ventana were dominated by *G. lucida* with *C. microstachya*, *C. diversifolia*, and *A. elemifera* as subdominants respectively, and the dwarf coastal forest was dominated by the pair *P. albida* - *E. fruticosa.* Another significant result of the comparative analysis of species composition between sites is that 9 species were only recorded in the Northern Slope, 3 species only in the Ridge, 3 in Lluberas, 2 in Ventana and 12 in the Coastal site (Table 3).

A multivariate correlation analysis using IVI values as the characterizing parameter showed that the upland forests were significantly correlated, particularly Guánica Ridge, Lluberas, and Ventana, whereas the Coastal site was clearly separated from the rest (bottom Table 3).

The relationship between the logarithm of % IVI and the species rank reveals patterns of community organization. Models vary from strong species dominance to random niche boundary, and log-normal distributions (Whittaker 1965). In species-rich communities, or samples combining species from a range of environments and communities, this relationship conforms commonly to a log-normal distribution. The communities analyzed in the five Guánica sites discussed above showed a nearly linear relationship between the log % IVI and

TABLE 3. Similarities in species number and composition of vegetation plots measured at different sites within the Guánica Forest (Codi: *Coccoloba diversifolia*; Bubu: *Bucida buceras*; Gylu: *Gymnanthes lucida*; Comi: *Coccoloba microstachya*; Amel: *Amyris elemifera*; Pial: *Pisonia albida*; Erar: *Erythroxylon areolatum*). Northern Slope after Molina (1988), Guánica Ridge, and Southern Slope after Van Bloem (1999). Below the non-parametric correlations between sites based on IVI (* p<0.01; ** p<0.001).

			Southern slope		Dwarf Coastal
	Northern Slope	Guánica Ridge	Lluberas	Ventana	(this study)
Area sampled m^2	2000	1500	900	900	1020
Mean Altitude asl m	100	129	147	25	10
Vegetation height m	6.8	4.5			1.4
N° species	37	37	34	31	41
Exclusive species	9	3	3	2	12
Dominant species	Codi	Gylu	Gylu	Gylu	Pial
	Bubu	Comi	Codi	Amel	Erfr
Multivariate non-parametric correlations					
	Northern Sl.	G.Ridge	Lluberas	Ventana	
Dwarf Coastal	-0.14	0.16	0.05	0.05	
Northern Slope	-	0.30*	0.52**	0.46**	
Guánica Ridge		-	0.50**	0.57**	
Lluberas			-	0.58**	

the species rank, following a pattern commonly found in communities developing in harsh environments (Whittaker 1965) (Fig. 6). The number of species varied from 32 in Ventana to 41 in the coastal dwarf forest, and the range of % IVI values decreases from the North Slope forest to the Coastal forest. This may be interpreted as a higher degree of species dominance in the upland forests and a more even spread of % IVI in the coastal forest. The slope of the logarithmic regression may be used as an index of this behavior, larger slopes indicating higher degree of species dominance. However, comparisons of these curves using common statistical techniques are not warranted with these data (Whittaker 1965).

The linearity of the log %IVI vs species rank relationship suggest strong environmental stresses on these forests such as

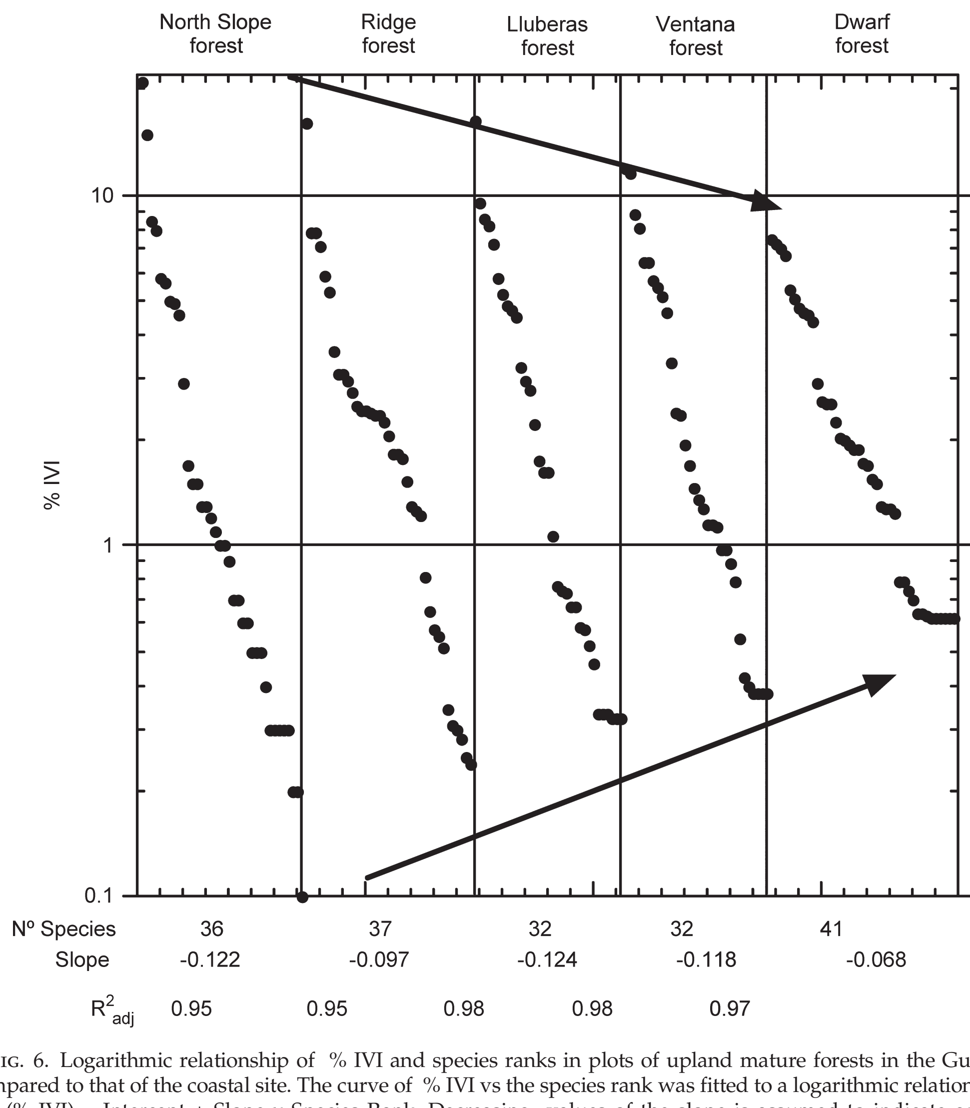


FIG. 6. Logarithmic relationship of % IVI and species ranks in plots of upland mature forests in the Guánica compared to that of the coastal site. The curve of % IVI vs the species rank was fitted to a logarithmic relationship: LN (% IVI) = Intercept + Slope x Species Rank. Decreasing values of the slope is assumed to indicate greater evenness in IVI distribution of the community (see text). The arrows highlight the changes in high and low % IVI values along the sequence from the Northern slope forest (Molina 1988), to the Guánica ridge forest, the Lluberas forest and the Ventana forest (Van Bloem 1999) and the dwarf forest of the present study. All R^2 significant at Prob>|t|<0.0001.

recurrent drought, and nutrient availability (Murphy and Lugo 1986). From the outset we have assumed that additional stresses such as Cooper, W. E. wind shearing, soil volumen, and salt spray, are constraining vegetation development at the coastal site, then why is there the dominance-species relationship not stronger developed? Our interpretation is that discontinuous substrate with regards to soil depth and scarcity of favourable sites for seedling establishment leads to a more even distribution of plant species. At the coastal sites it appears that tolerance to environmental stress and scarcity of space for establishment may play a more important role than interspecific competition modulating species composition and dominance.

Common species within the fives sites express a large morphological plasticity in overall structural development, mainly of those traits that allow development of shrubby habits under stress and full tree development under favorable conditions. The species of this type identified here as highly plastic are *E. areolatum, T. heterophylla, F. citrifolia*, *P. albida,* and *B. simaruba*. In addition, a strong selection for species with fleshy fruits, probably dispersed by animals, seems to be operating in the formation of the dwarf coastal forest.

The group of species restricted to the dwarf coastal forest includes several shrubs or small trees, capable of growing root systems through the crevices of the calcareous substrate such as *B. krugii, C. indica, C. costata, C. rigidus* and *M. tomentosa*. In addition we found specialists resistant to soil water salinity (*C. erectus*) or sea salt spray (*S. maritima, C. uvifera, J. armillaris*).

The results on species composition, structure, species dominance spread, and plot heterogeneity support the conclusion that the dwarfed coastal vegetation in Guánica Forest does not constitute a phytosociological unit, but represents the terminal community type in an environmental gradient from the upland dry forest stressed by irregular water supply and nutrient availability to a vegetation tolerant to additional environmental stresses such a soil salinity and salt spray.

Acknowledgements.—To Miguel Canals, manager of the Guánica Biosphere Reserve, for his help in selecting sites and supporting research activities in the area and Skip Van Bloem (University of Puerto Rico, Mayagüez) who made valuable comments that helped to improve the manuscript. To the students participating in the plant ecology class of the Pontificial University of Puerto Rico for their contribution to the plot survey. To the reviewers of the CJS for extensive critical comments that lead to a full restructuration of the original paper. This research was conducted in cooperation with the University of Puerto Rico.

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