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Students from Wesleyan University conducting field work for the article by Dong and Knorr in this volume of **Acta**. The photos were taken by Professors Timothy Ku and Phillip Resor.

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TABLA DE CONTENIDO

ARTICULOS

ENSAYOS

EDITORIAL

Por segunda vez, **Acta** publica artículos de estudiantes de cuarto año de Wesleyan University en Middletown, Connecticut. Los trabajos se llevan a cabo como parte de un seminario para estudiantes que están finalizando sus bachilleratos. La clase viaja a Puerto Rico para llevar a cabo los trabajos de campo y bajo la dirección de su profesor el Dr. Dana Royer del Departamento de *Earth and Environmental Sciences* analizan los datos y desarrollan los manuscritos al regresar al campus de Wesleyan. Los trabajos iniciales aparecen en el volumen 24 de **Acta**. En este número también incluimos un trabajo por la estudiante subgraduada de la Universidad de Puerto Rico en Río Piedras, Gabriela M. Morales. Es la intención de esta revista el proveer espacio para que estudiantes universitarios y no universitarios y sus maestros publiquen los trabajos que llevan a cabo como parte de sus cursos en sus respectivas escuelas y universidades. Adelantamos que el próximo volumen de **Acta**, el cual celebra los 30 años de publicación consecutiva de la revista, estará dedicado a trabajos por maestros y estudiantes de la Universidad de Puerto Rico, recinto de Río Piedras. Invitamos a otras facultades de escuelas y universidades a aprovechar la oportunidad que representa la disponibilidad de **Acta Científica** para divulgar los trabajos de investigación que llevan a cabo en sus ámbitos académicos. Aprovecho la oportunidad para agradecer a las siguientes personas que colaboraron con el Editor de **Acta** en la confección de éste volumen: Helen Nunci, Gisel Reyes, Gaby Joglar y los empleados de la Biblioteca Frank H. Wadsworth del Instituto Internacional de Dasonomía Tropical, Jorge Morales y Evelyn Pagán.

Ariel E. Lugo
Editor

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PETROLOGY, GEOCHEMISTRY, AND MORPHOLOGY OF THE LAPA LAVA PILLOW BASALTS, SALINAS, PUERTO RICO

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ABSTRACT

Well-preserved basalt pillows are exposed in a roadcut on Hwy 52, Salinas, Puerto Rico. The exposed pillow basalts were sampled and analyzed for bulk geochemistry as well as thin section petrology. A photo panorama of the outcrop was compiled and analyzed for pillow morphology. Pillow morphology suggests a constant low effusion of relatively high viscosity magma on a gently-inclined paleoslope. Glassy chilled margins and increasing grain size from pillow rim to core indicates rapid quenching of pillow rims followed by relatively protracted crystallization of pillow interiors. Geochemical analysis of major and trace element composition suggests the origins as a tholeiitic melt near the Benioff zone, consistent with the Lapa Lava Member of the Robles Formation. Despite an abundance of secondary alteration phases in rim and near-rim zones of the pillows there is no significant change in major element geochemistry that can be traced to seawater alteration.
Keywords: pillow basalts, Robles Member, elemental chemistry, andesite.

RESUMEN

Las almohadas de basalto bien conservadas están expuestas en un corte de ruta en la autopista 52, Salinas, Puerto Rico. Se tomaron muestras de las almohadas de basalto expuestas y se analizaron para la geoquímica mayor y la petrología de las secciones delgadas. Una foto panorámica del afloramiento fue recopilada y analizada por la morfología de las almohadas. La morfología de las almohadas sugiere un bajo derrame constante de alta viscosidad del magma en un *paleoslope* de pendiente suave. Los márgenes refrigerados vidriosos y el aumento del tamaño del grano desde el borde hasta el centro de las almohadas indican un enfriamiento rápido de los bordes de las almohadas, seguido de la cristalización relativamente prolongada de los interiores de las almohadas. El análisis geoquímico de las composiciones de los elementos mayores y trazas sugiere que los orígenes son una masa fundida toleítico cerca de la zona de Benioff, que es consistente con el miembro Lapa Lava de la Formación Robles. A pesar de la abundancia de las fases de alteración secundaria en las zonas en y cerca del borde de la almohada, no hay un cambio significativo en la geoquímica de los elementos importantes que se puede remontar a la alteración del agua del mar.
Palabras clave: almohadas de basalto, Formación Robles, química elemental, andesita.

INTRODUCTION

The Lapa Lava Pillow Basalts are part of the Robles Formation in Puerto Rico's central igneous province, which ranges from Early to Late Cretaceous high potassium basalts and andesites (Jolly 1971). Previous geochemical studies by Schellekens (1998) have shown that the central igneous province has Cr/Y and Ti/Zr ratios and a slight enrichment in LREE consistent with island arc magmatism. The central igneous province is overall consistent with island arc tholeiites. The Robles Formation has variable SiO_2, high Sr, and high total alkalis. The Lapa Lava Pillow Basalts in particular have higher K_2O and P_2O_5 (Jolly 1971, Schellekens 1998), although detailed chemical analyses had not been conducted.

The pillow basalts in Salinas, Puerto Rico are well-formed, large pillow structures. Hart (1969) studied seawater alteration of pillow basalts in the Puerto Rican trench and found that altered samples had higher H_2O concentrations and high ratios of Fe_2O_3 to FeO in pillow rims relative to the cores. Additionally, pillow rims were depleted in SiO_2 and enriched in K_2O relative to pillow centers (Hart 1969, 1970). A study of the Robles Formation (Jolly 1971) suggests that the Salinas pillows are part of the Lapa Lava Member of the Robles Formation, and thus are part of a calc-alkaline basaltic-andesitic series that formed as a ~20% partial melt of primitive mantle from the Benioff zone. The Lapa Lava Member is comprised of six different flow units, commonly associated with pillow structures present in several members. Lapa Lava outcrops rarely have vesicles, glass, or volcanic breccias. Clinopyroxenes in the Lapa Lava Member, which are subhedral unzoned augites, are similar throughout. Many of the units of the Lapa Lava Member are highly enriched in K, unlike other rocks in the region, and are geochemically similar to each other (Jolly 1971). Based on data from Hart (1969), we predicted that the pillow basalts exposed at Salinas would be part of the Lapa Lava flows, and would show decreased silica and increased K, Mn, Fe_2O_3, and water from the pillow core to its rim.

We measured pillow morphology in the outcrop to provide insight into the conditions during emplacement, including cooling rate, magma viscosity, effusion rate, and slope of emplacement. Thin section petrography was used to investigate textural variations that result from the cooling process, as well as the crystallization history of the source magma prior to eruption. Geochemical analysis of major and trace element compositions of samples taken from pillow rims and cores sheds light on post-eruptive chemical alteration of the pillows. These data may also be used to identify the source magma within the context of other Caribbean basalts.

METHODS

Outcrop Description

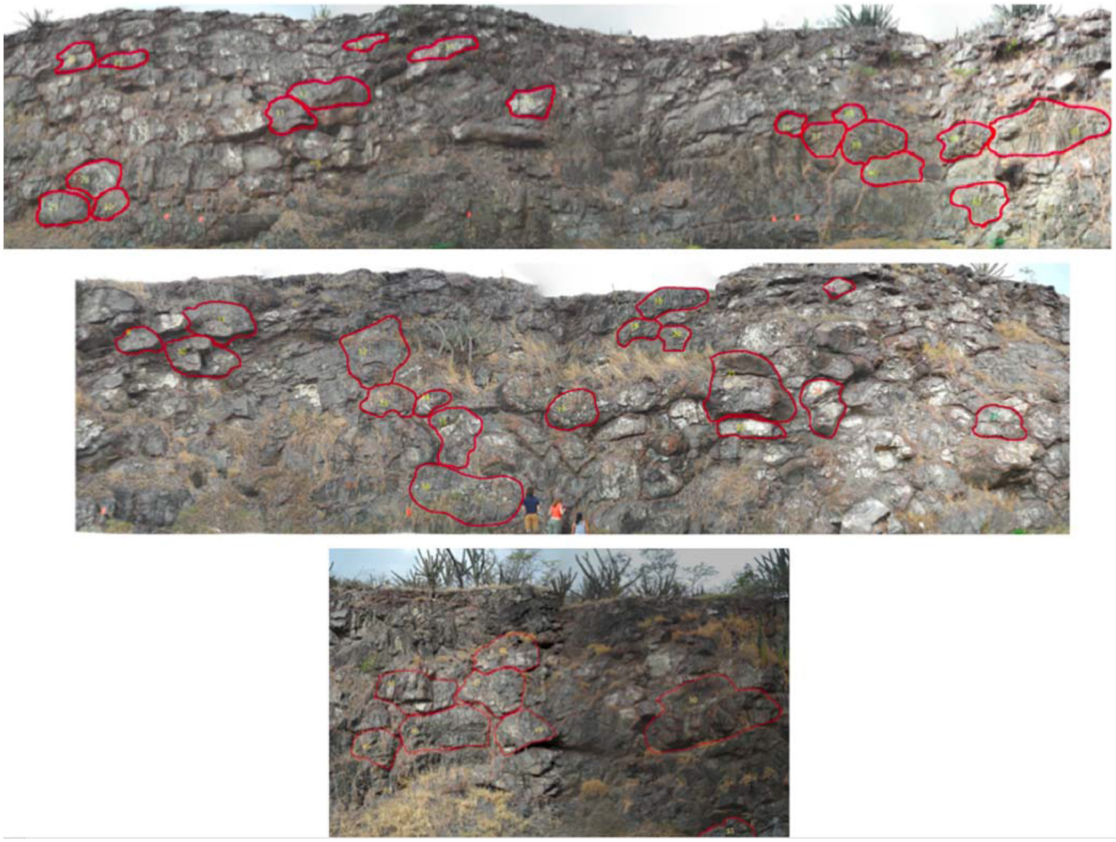
The pillow basalts sampled are well exposed in a roadcut along Route 52 near Salinas, Puerto Rico (Figs. 1-2). The outcrop is exposed for approximately 60 m; individual pillows are clearly visible, separated by highly altered layers of serpentinized volcanic glass. Many pillows have radial joints from the center outward. More elongated pillows have a center fracture parallel to the long axis, with smaller joints radiating outward toward the rim.

Field Methods

To study morphology, photos were taken of the entire outcrop at a standard distance of 440 cm from the outcrop. Samples were collected using a 25-mm diamond core bit; cores were taken from two pillows at four locations across each pillow's radius. The cores were taken from the rim, just inside the rim, midway between the rim and core of the pillow; and the

Figure 1. Satellite image of Puerto Rico showing the location of the pillow basalts studied (modified from Google Earth; © ESRI 2016).

Figure 2. Outcrop panoramas, with the pillows measured for maximum and minimum length outlined in red.



core of the pillow. For the rim and rim interior samples of the first pillow, a hand sample was broken off rather than a drilled core.

Spatial Analysis

We used Hugin software to construct a photomosaic of the entire outcrop. Greatest and least axes were then measured in Photoshop and aspect ratio was determined. Morphology was interpreted following the methods of Schnur (2007).

Geochemical and Petrographic Analysis

Samples were prepared for XRF using a jaw crusher, shaker box, and mortar and pestle to homogenize the samples. XRF major and trace analyses were conducted at University of Massachusetts by J. Michael Rhodes. Thin sections were made by National Petrographic (Houston, TX) and analyzed using an optical microscope.

RESULTS

Morphology

The roadcut provided an excellent cross-sectional view of pillow basalt structure. Each pillow observed at the outcrop had dis-tinct chilled margins (Fig. 3), as well as a high volume of matrix. The intact pillows studied at the outcrop were notably rough-surfaced. Pillow basalts of the Lapa Lava Flow were found to be of similar size and did not vary significantly in size throughout the horizontal length of the outcrop. There was a slight decrease in size from bottom to top of the outcrop.

Generally, the pillows were slightly elongated in the horizontal. The average maximum axis was 1.8 m and the average minimum axis was 1.0 m. The average values indicate slightly elongated pillows. Maximum axes ranged from 0.73 m to 4.5 m, and the

FIGURE 3. Chilled margins about 5 cm thick are distinct at the rim of each pillow. Note the radial fractures within the pillow associated with protracted cooling and shrinkage of pillow cores.

minimum axes ranged from 0.4 m to 2.1 m. A plot of the maximum vs. minimum dimensions shows that most of the pillows have roughly the same proportions and fall near the average size (Fig. 4). The standard deviation for the aspect ratios (length/width) was 0.66, indicating little variation in pillow diameter. The median maximum dimension was 1.70 m and the median minimum axis was 0.93 m (Table 1).

In general, the horizontal axes of the pillows tended to be larger than the vertical axes at our site. Aspect ratios ranged from 1.02 to 3.62, with an average of 1.93 and median of 1.86. Relatively large aspect ratios indicate less rounded and more elongated along the maximum/horizontal axis, and thus indicate a gentle paleoslope (Schnur, 2007). On a plot of the axes against the aspect ratio, there was no relationship between the aspect ratio and the length of either axis (Fig. 5). Furthermore, there was a small decrease in aspect ratio with increasing vertical height (Fig. 6).

Thin Section Petrography

Thin sections were made for all eight samples (see Fig. 7 for representative micrographs). All samples had a porphyritic texture, with aphanitic groundmass with small laths and large

Figure 4. Maximum and minimum pillow dimensions for 56 pillows (blue diamonds), and average maximum and minimum axes (red square).

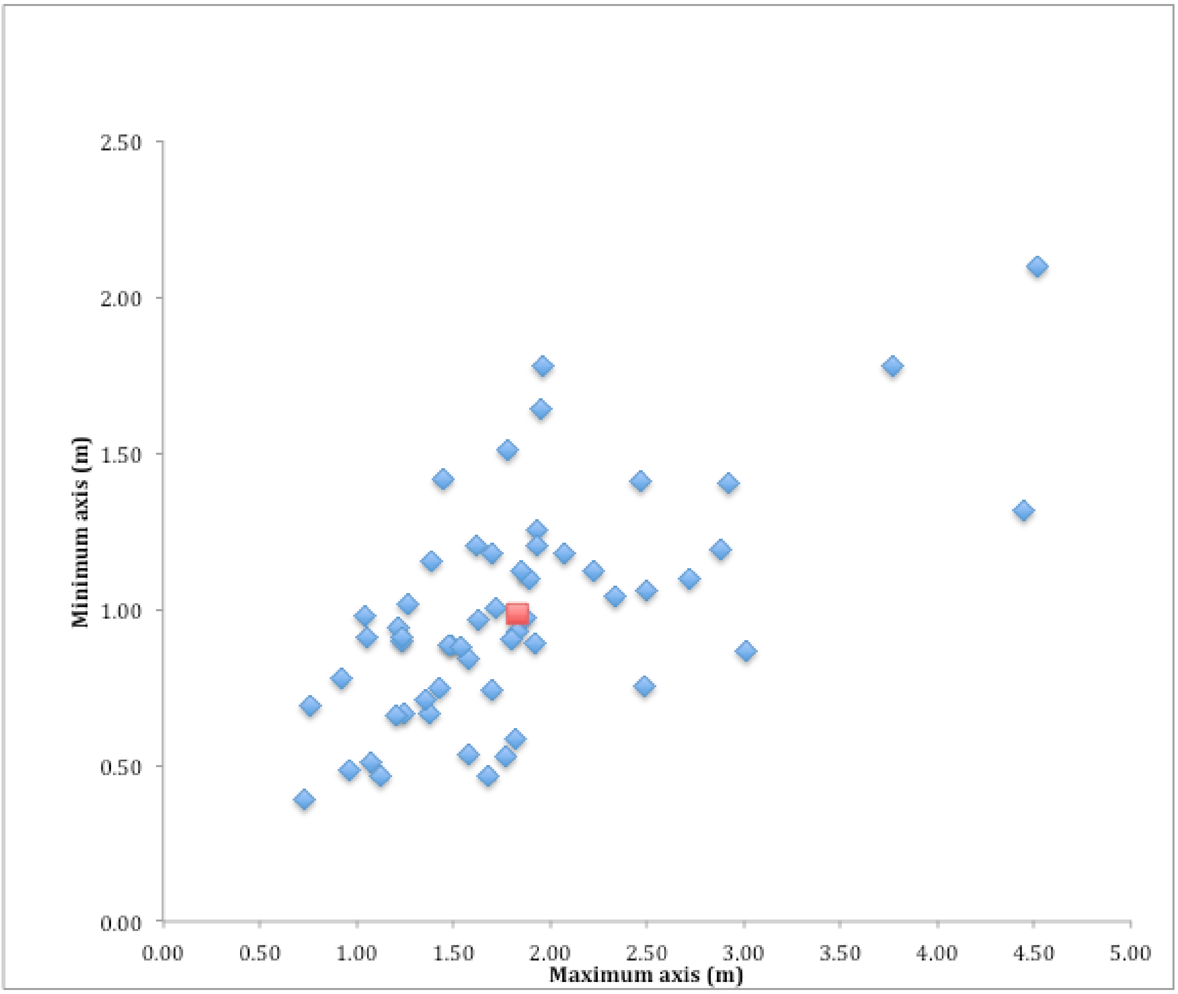


Table 1. Major element composition (in weight percent) of the analyzed samples. *Fe_2O_3 represents total ferric iron.

	SiO_2	TiO_2	Al_2O_3	Fe_2O_3*	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	Total
P1A	51.79	0.79	15.82	8.33	0.20	5.95	10.17	2.98	3.48	0.46	99.97
P1B	50.69	0.78	15.51	8.43	0.18	5.40	12.35	2.83	3.09	0.47	99.73
P1Cc	53.90	0.82	17.12	7.38	0.16	5.13	7.83	3.11	3.68	0.44	99.57
P2Aa	52.56	0.83	16.54	7.99	0.17	5.91	8.22	3.28	3.95	0.45	99.90
P2Bb	51.74	0.77	15.13	8.43	0.19	5.67	11.33	3.19	3.18	0.45	100.08
P2Cb	55.07	0.86	16.46	8.01	0.16	5.63	5.56	4.19	3.45	0.46	99.85
P2D	53.59	0.79	15.52	8.48	0.17	5.72	8.63	3.31	3.28	0.43	99.92

Figure 5. Minimum and maximum axes show no correlation with pillow aspect ratio.

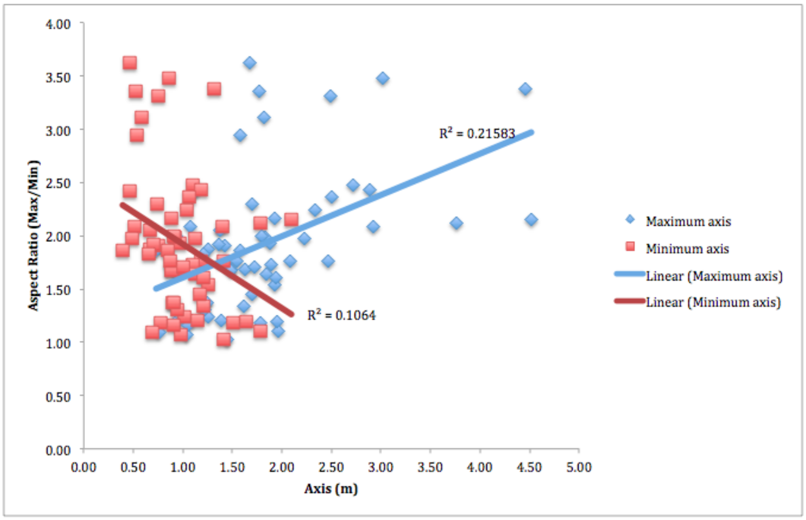


Figure 6. Inverse relationship between aspect ratio and increasing vertical position of the pillow. Higher aspect ratios correspond to position further down in the section.

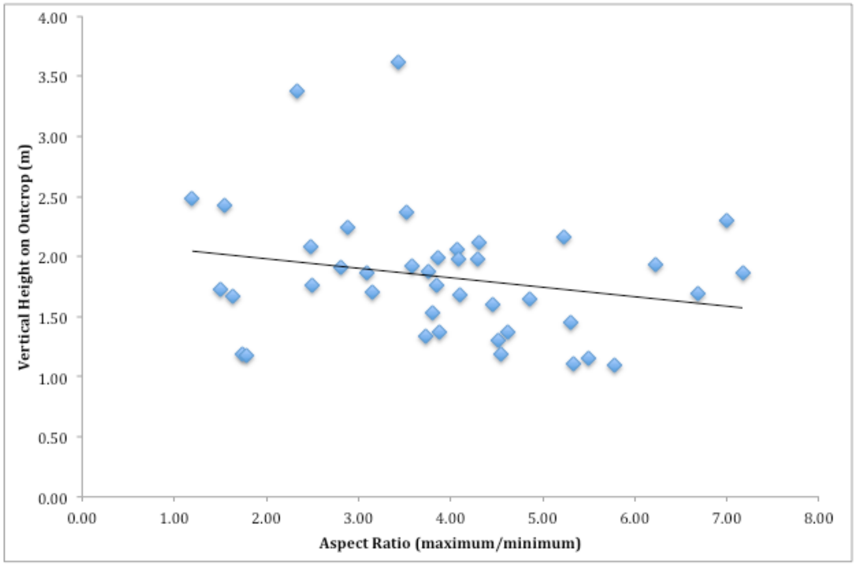
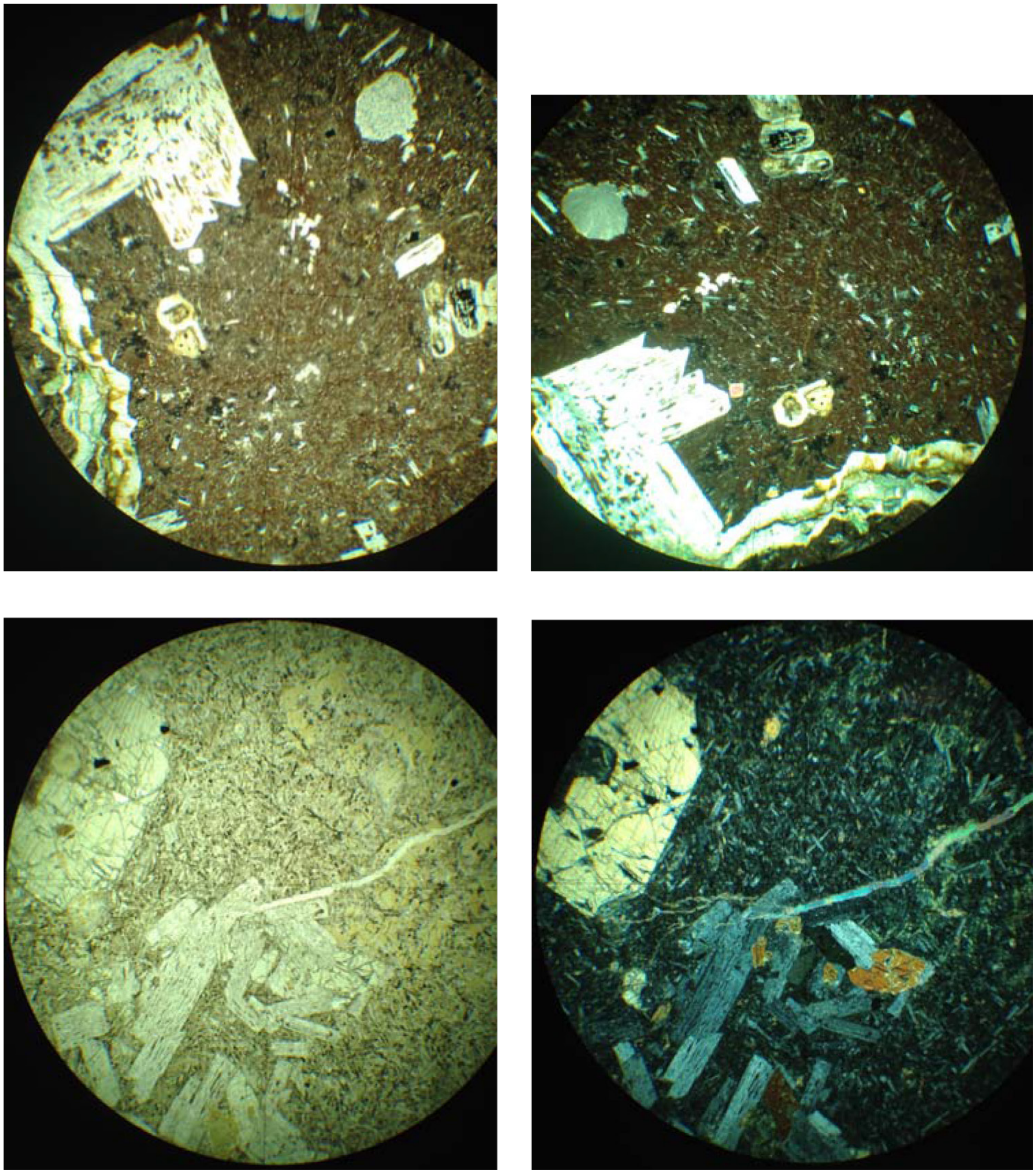


Figure 7. Thin section micrographs of (clockwise from top left) P2 rim PPL pillow, P2 rim CPL pillow, P2 core PPL pillow, and P2 core CPL pillow. Rims have cryptocrystalline/glassy groundmass with significant secondary alteration, especially of ferromagnesian minerals and glass. Sieve texture of K-feldspar phenocrysts suggests disequilibrium crystallization. Fractures are significantly chloritized, indicating relatively high-T remineralization post-emplacement. Pillow cores are relatively unaltered, with intact K-feldspar phenocrysts and glomerporphyritic plagioclase and augite. Plagioclase microphenocrysts are significantly larger in groundmass; optically resolvable augite microcrysts are present in groundmass, which is significantly less glassy than pillow rims.



(0.5-3 mm) orthopyroxene, clinopyroxene, and plagioclase glomeroporphyritic phenocrysts. The plagioclase laths have opaque glass inclusions generally oriented along the cleavages of the phenocryst. There are highly serpentinized/chloritized bipyramids with a symplectic corona of plagioclase that may be relict olivine phenocrysts. Pyroxenes include high-Mg and high-Fe pigeonite phases, both euhedral and occasionally twinned with each other. Euhedral augite phenocrysts occur in similar abundance to the pigeonite and plagioclase. Some of the feldspar laths may be sanidine, based on lack of polysynthetic twinning and the high K composition of the bulk rock, but the laths are generally too altered and disrupted by glass inclusions to be definitively identified optically.

The groundmass of the sections shows significant changes in grain size and mineralogy from pillow rim to core. Pillow rims are highly weathered, with near-opaque Fe oxides and trachytic plagioclase microcrysts. Fractures in pillow rims are filled with calcite, and some phenocrysts are replaced with calcite. Across the radius of the pillows, from rim to center, groundmass crystal size increases, with plagioclase microcrysts nearly tripling in length. In the pillow centers, the groundmass is not nearly as weathered, and as crystals are larger, other phases become visible, including pyroxene laths and opaque prisms and needles. The groundmass is no longer trachytic, and microcrysts are oriented randomly.

Major and Trace Element Geochemistry

Seven of the eight samples were analyzed for major and trace elements using XRF. These pillows had an intermediate SiO_2 composition and unusually high K_2O, as well as fairly high Na_2O and CaO relative to a typical basaltic andesite (Table 2). There were no significant geochemical trends from the rim to the core of the pillows. The range in oxide concentrations varied by less than 10% of the individual concentrations throughout all samples. Analytical error was less than 0.5%. The trace element composition of these samples did not vary significantly from rim to core, excepting high La values in the rim of pillow 1 relative to the other samples (Table 3). Heterogeneity in trace element concentration is limited to normal variation caused by analytical error and small sample sizes. The samples were highly enriched in large-ion lithophile elements (LILE) and high field strength elements (HFSE), especially Rb, Ba, Pb, Sr, and Th. There was no U detected in the samples; this was unexpected considering the pillows' enrichment in other HFSE, and may be the result of analytical error.

DISCUSSION

Morphology

Morphological study of pillow basalts can infer the conditions under which the pillows were formed. Parameters that have been determined from pillow shape include cooling rate, lava viscosity, effusion rate, and slope of emplacement. Gregg and Fink (1995) described pillow growth as a relationship between rate of lateral growth, rate of extrusion, rate of cooling, rate of solidification, and plastic spreading downslope. The primary control on pillow growth is cooling rate, which is affected by the water temperature, lava temperature, and effusion rate. Pillows usually form at higher cooling rates when the difference between the lava temperature and water temperature is high, characteristic of pillows forming in deep ocean water (Schnur 2007). The thickness of the fine-grained chilled margins around the pillows is a measure of the relative cooling rate; the faster the cooling rate, the more distinct the chilled margins (Dimroth et al. 1978). The observed distinct margins around the pillows indicate rapid cooling. In addition, there is a high volume of interpillow matrix, which also

Table 2. Minor and trace element compositions of the seven pillow samples. All values in ppm. U was below detection.

ppm	P1A	P1B	P1Cc	P2Aa	P2Bb	P2Cb	P2D
Rb	43.0	34.1	49.6	58.0	37.6	43.0	40.4
Ba	1446	1301	1844	1811	1320	1439	1395
U	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Nb	3.5	3.5	3.9	3.7	3.3	3.7	3.3
La	21	9	8	8	7	9	9
Ce	23	21	24	24	22	25	22
Zr	86	83	93	91	82	93	87
Pb	7	10	9	5	7	6	7
Sr	559	457	583	614	526	597	583
Th	3	3	3	2	3	3	3
Ga	14	15	16	16	14	16	14
Zn	92	79	62	69	69	65	71
Ni	118	107	78	87	114	81	120
Cr	275	332	197	231	398	196	363
V	225	235	234	237	223	225	232
Y	14.6	14.8	15.8	15.4	14.3	15.7	14.7
P	100000	102174	95652	97826	97826	100000	93478

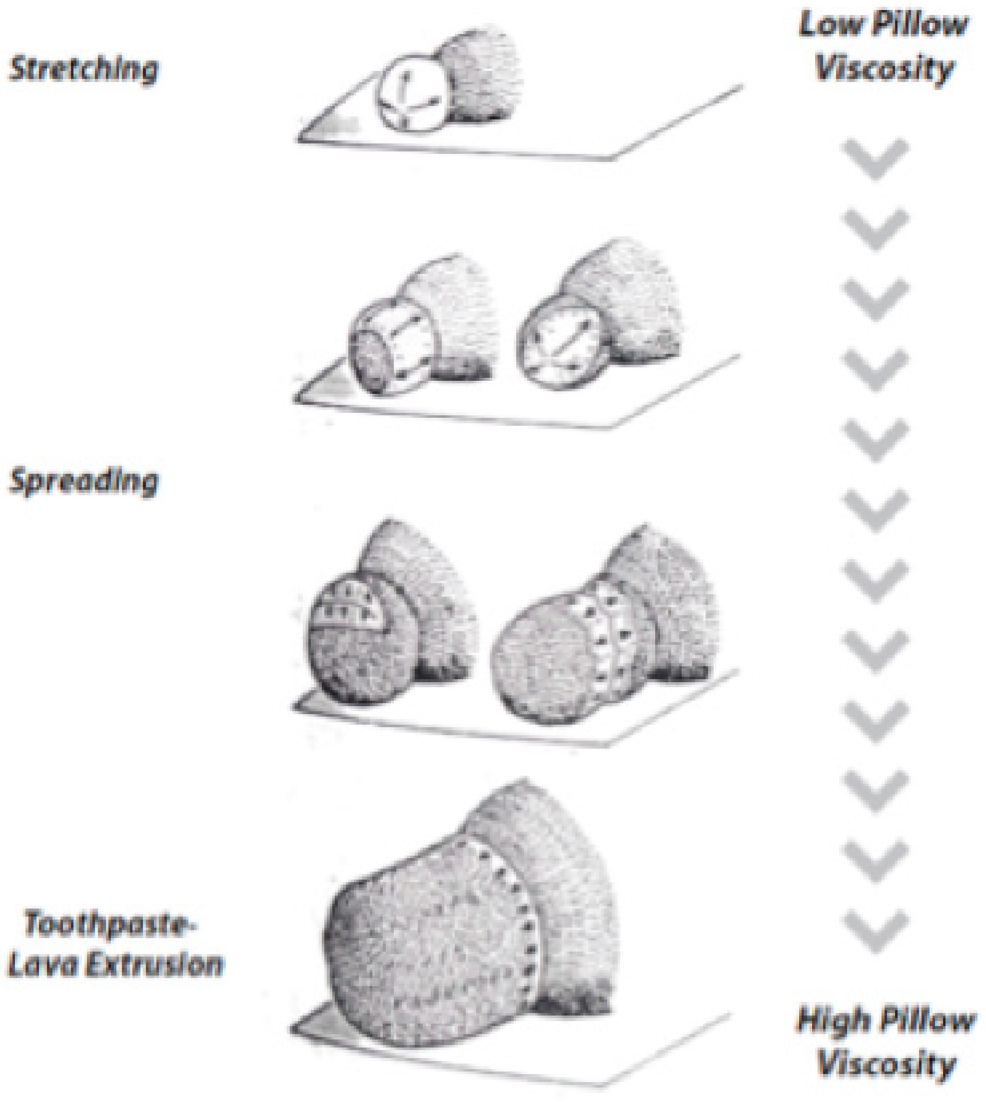
Table 3. Central tendencies and aspect ratio of pillows.

	Max (m)	Min (m)	Aspect Ratio (Max/Min)
Average	1.83	0.99	1.93
Standard Dev	0.79	0.36	0.66
Maximum	4.52	2.09	3.62
Minimum	0.73	0.39	1.02
Median	1.70	0.93	1.86

indicates fast quenching of the rims (Swanson and Schiffman 1979).

Lava viscosity also affects the growth rates of pillows and determines the average pillow size (Schnur 2007). Walker divided pillow growth into four categories that are related to lava viscosity (Fig. 8; Walker 1992, in Schnur 2007). These mechanisms varied from stretching of the chilled skin of low viscosity lavas to toothpaste-like lava extrusion of high viscosity lavas. Higher viscosity lavas also have a slower pillow growth rate, which leads to larger pillow size (Schnur 2007). The notably rough surfaces of the Lapa Lava pillows suggest a relatively high viscosity. Pillows with high viscosity extrude at slow rates and usually have grooves caused by the scraping against the opening from which they are budded (Schnur 2007).

FIGURE 8. Walker's classification of pillow growth related to increasing lava viscosity. The first mechanism is characterized by uniform localized stretching of the chilled, relatively smooth skin. Pillows of the highest viscosity grow by toothpaste-like extrusion where lava is pushed from the solidified pillow; these pillows are usually rough surfaced. (Schnur 2007).



The rate of lava extrusion from the vent can impact pillow size. Changes in effusion rate can result in shifts in pillow size through the vertical cross-section of the pillow sequence (Dimroth 1978; Schnur 2007). The upward decrease in pillow size of the Lapa Lava basalts suggests a decrease in effusion rate over the eruption period. The sizes of the pillows and the rough surfaces on their margins also suggest lower effusion rates and higher viscosity. Additionally, the similitude of pillow sizes throughout the outcrop also suggests relatively constant effusion rates.

Lastly, the slope on which the pillows are emplaced is a factor in determining pillow morphology. Generally, pillows form on gentle to moderate slopes because gravity doesn't cause as extensive deformation as it does on steeper slopes. Larger, more rounded pillows form on gentle slopes whereas smaller, more elongated pillows form on steeper slopes. Higher aspect ratios mean that the pillows are more elongated than they are rounded, which was the case for the Puerto Rican pillows. The pillow sizes and high aspect ratios suggest a gentle incline of the paleoslope.

Petrology

The high temperature phases found in thin section—sanidine and Mg-rich augite—are accompanied by equivalent lower temperature phases, including Fe-rich pigeonite, suggesting the source magma underwent a period of fractional crystallization at depth and again closer to the surface, prior to eruption. Partial resorption of relict olivine phenocrysts supports storage at temperatures and pressures below olivine stability, and the aforementioned bimodal distribution of feldspar and pyroxene phases suggests mixing of thermally and chemically distinct magmas shortly prior to eruption (Thornber 2001).

Geochemistry

The major element geochemistry of this pillow basalt flow is consistent with previous analysis of the Lapa Lava Member of the Robles Formation (Jolly 1971; Fig. 9). The unusually high K_2O, high Al_2O_3, low TiO_2, and enrichment in LILE and HFSE of this member, in addition to high-temperature phases in the phenocryst assemblage of the Lapa Lava pillows, characterize it as a shoshonite. Shoshonites are a relatively rare high-K equivalent of calc-alkaline basaltic-andesitic volcanics that are associated with island arcs and continental margins (Morrison 1980; Li et al. 2000). The Lapa Lava, and by extension the rest of the Robles Formation, is likely associated with the a calc-alkaline magma developed from a tholeiitic basalt pile, similar to the other arc rocks found in Puerto Rico's central igneous province. Petrographic evidence for magma mixing suggest this particular member formed from heating of a high-K_2O shallow reservoir by injection of a mafic melt from a deeper, high-temperature source.

The trace element assemblage of these pillows shows enrichment in LILE relative to primitive mantle and N-MORB, typical of island-arc shoshonites (Fig. 10). There was no detectable U in the samples, which is more likely related to analytical error than actual lack of U. Jolly (1971) found ~1.5ppm U in four of the six flows, suggesting these flows are in fact enriched in U along with the other HFSE and LILE. Although the rims are highly weathered and have undergone mineralogical alteration, trace element composition does not vary greatly from rim to core, suggesting the pillow basalts did not undergo significant seawater alteration.

Based on slightly elevated Fe_t relative to shoshonites associated with calc-alkaline series, these flows appear to be sourced from a tholeiitic magma near the Benioff zone, and was either assimilated with a high-K reservoir or was simply a product of a low degree of partial melting (Morrison 1980; Schellekens 1998).

CONCLUSIONS

Chilled margins and abundant interpillow matrix indicate the Lapa Lava pillows of the Robles Formation were quenched rapidly upon extrusion. The pillow sizes and rough surfaces indicate lower effusion rates and high viscosity; the high aspect ratios suggest a gentle incline for the paleoslope. The homogeneity of pillow sizes display evidence for a constant effusion rate, with a slight decrease toward the top of the section. LILE and HFSE enrichment

Figure 9. Total alkalis vs. silica IUGS classification diagram. Orange – this study of the Lapa Lava pillows; blue - six Lapa Lava flows, Jolly (1971).

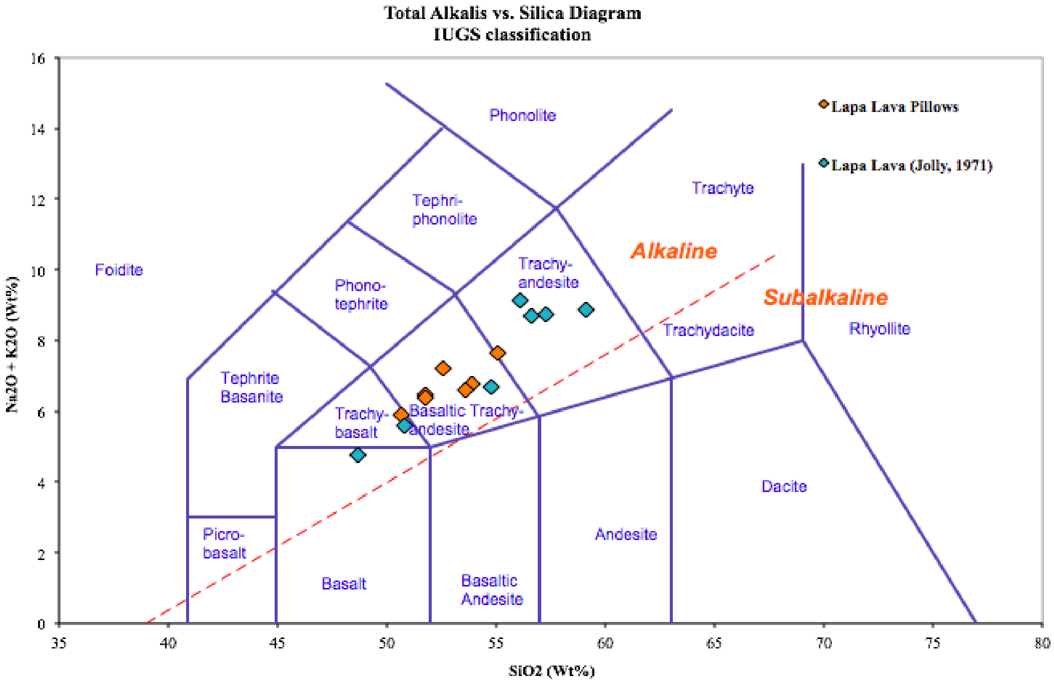
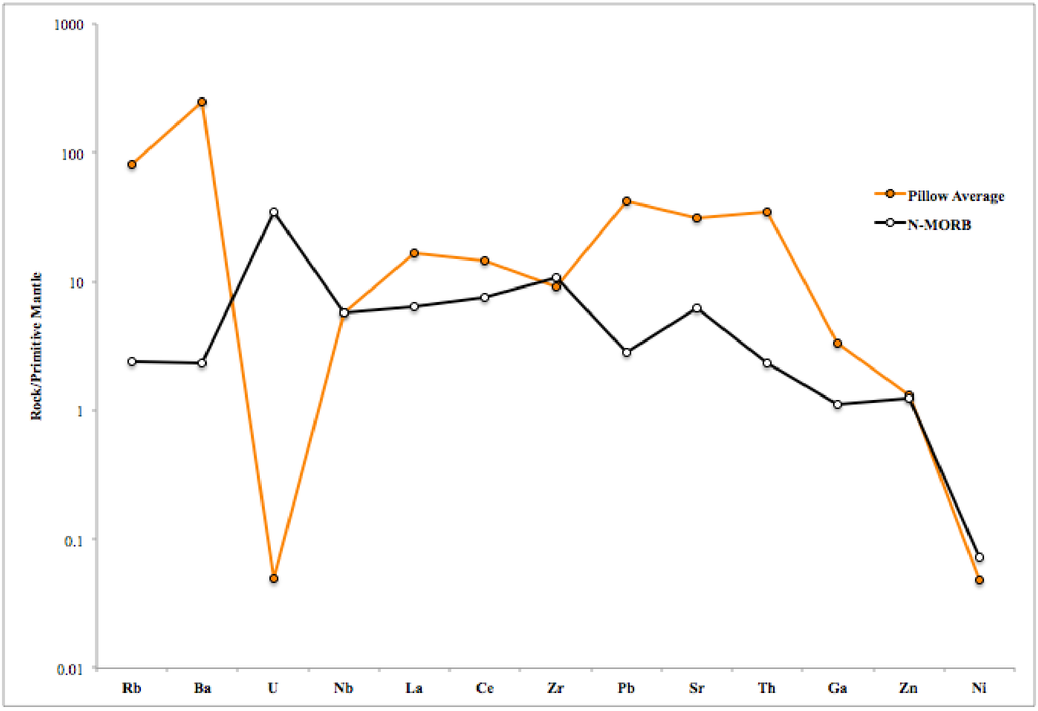


Figure 10. Trace elements in the 2014 Lapa Lava pillows and N-MORB, normalized to primitive mantle. N-MORB and primitive mantle compositions from Halliday et al. 1995; Hofmann 1988; Sun 1982. U was not detected in the analyses but is assumed to be present in very low concentration. Despite apparent U depletion, the pillow lava is enriched overall in HFSE and LILE relative to N-MORB.



suggests a relatively low degree of partial melting of dry mantle under high pressure. The geochemistry and petrology of these pillows is consistent with the Lapa Lava member of the Robles Formation, a Cretaceous suite of arc rocks. The Lapa Lavas are a shoshonitic basaltic andesite, likely originating from a tholeiitic melt near the Benioff zone.

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GEOCHEMICAL EVIDENCE FOR THE ORIGIN OF MARINE TERRACE SOILS IN NORTHERN PUERTO RICO

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ABSTRACT

The long-range transport and deposition of dust from Africa is a critical process in the formation of nutrient-rich soils on several Caribbean islands including Jamaica, Barbados, and the Bahamas. These islands are largely comprised of carbonate rocks with outside sources playing an important role in soil development. Puerto Rico consists of approximately 1/3 carbonate and 2/3 igneous bedrock leading to different mechanisms of soil production. Potential parent materials for Puerto Rican soils include African dust, local igneous rocks, Mississippi loess, and volcanic ash. This study evaluates the significance of African dust and other parent materials by sampling soils on marine carbonate terraces along the northern coast of Puerto Rico. Parent materials are differentiated according to immobile element ratios (Al_2O_3/TiO_2, Ti/Y, Ti/Zr, and Ti/Th) and rare earth element chemistries. Results show that local igneous rock provides the most significant parent material for soils developed on marine terraces. Nearby volcanic sources from the Lesser Antilles and Dominica – St. Lucia also appear to be potential contributors. African dust is considered to be an insignificant source as the weathering rate of local igneous rock outweighs the deposition rate of African dust. These findings suggest a difference in soil formation mechanisms between Puerto Rico and those of other Caribbean islands.
Keywords: African dust, marine terraces, rare earth elements, soils.

RESUMEN

El transporte a larga distancia y la deposición de polvo de África es un proceso crítico en la formación de suelos ricos en nutrientes en varias islas del Caribe, como Jamaica, los Barbados y las Bahamas. Estas islas están compuestas en gran parte de las rocas carbonatadas con fuentes externas que son importantes para el desarrollo del suelo. Puerto Rico se compone de aproximadamente 1/3 lecho de roca carbonato y 2/3 lecho de roca ígnea que conducen diferentes mecanismos de producción del tierra. Los materiales paternales potenciales para los suelos de Puerto Rico incluyen polvo africano, rocas ígneas locales, loess Mississippi y la ceniza volcánica. Este estudio evalúa la importancia del polvo africano y otros materiales paternales tomando muestras del suelo en las terrazas de carbonatos marinos a lo largo de la costa norte de Puerto Rico. Se diferencian los materiales paternales de acuerdo a las proporciones de los elementos inmóviles (Al_2O_3/TiO_2, Ti/Y, Ti/Zr, and Ti/Th) y la química de elementos raros de tierra. Los resultados muestran que la roca ígnea local proporciona el material base más importante para los suelos desarrollados sobre las terrazas marinas. Fuentes volcánicas de Lesser Antilles y Dominica - Santa Lucía también parecen ser posibles contribuyentes. El polvo africano es considerado como una fuente insignificante porque la tasa de erosión de las rocas ígneas locales es mayor que la tasa de deposición de polvo africano. Estos hallazgos sugieren una diferencia en los mecanismos de la formación del suelo entre Puerto Rico y el de otras islas del Caribe.

Palabras clave: polvo de África, terrazas marinas, lantanoides, suelos.

INTRODUCTION

Puerto Rico and its neighboring Caribbean islands have large areas underlain by carbonate bedrock (Larue et al. 1998). Yet, carbonates themselves do not contribute significantly to the soil fertility of these islands. For instance, Muhs et al. (1987) showed that geologically unreasonable amounts of limestone would be required to generate the clay-rich soils on Barbados. In addition to lacking essential nutrients (N, P, K), calcium carbonate can concentrate into hard, impermeable layers which can impede water movement as well as plant roots (Alcantara 2007). Several possible modes of soil formation on carbonate islands in the Caribbean region have been proposed by previous studies, one of which is the long-range transport of dust from Africa (Muhs and Budahn 2009).

While the northern coast of Puerto Rico is predominantly underlain by carbonates, the central portion of the island is dominated by igneous rock provinces at higher elevations (Fig. 1). Thus, soils developed on northern carbonate bedrock units could be derived from both local and distant sources. This paper examines trace element and rare earth element (REE) ratios to determine the origin of soil components developed on the carbonate marine terraces along the northern coast of Puerto Rico.

Soil parent materials can be identified using trace element and REE ratios. These elements are good tracers because they are relatively immobile and retain their chemical identities despite considerable chemical weathering involved in the formation of Caribbean soil (Muhs et al. 1990). REEs occur in predictable concentrations throughout Earth's crust as a result of differences between tectonic, magmatic, and metamorphic processes (Davranche 2009). The ratio of two immobile elements can act as a geochemical fingerprint for African dust and other parent materials.

Potential Parent Materials

The aluminosilicate fraction of northern Puerto Rico soil could be derived from 1) African dust, 2) Mississippi loess, 3) volcanic ash from Caribbean volcanoes, or 4) nearby igneous rocks from central and northeastern Puerto Rico. The annual amount of global dust emissions from desert sources is estimated at approximately two billion tons (Moulin et al. 1997). African dust picked up from the Sahara and Sahel desert regions of North Africa can travel at altitudes of nearly 4 km across the Atlantic, depositing large amounts of dust onto the Caribbean islands (Muhs et al. 2007). A previous study examining the nutrient inputs in the Luquillo Mountains of Puerto Rico found that half of the phosphorous in the soil and biomass is derived from dust deposition (Pett-Ridge et al. 2009). Additionally, geochemical evidence from nearby Barbados, Jamaica, and the Florida Keys shows North African dust as a significant

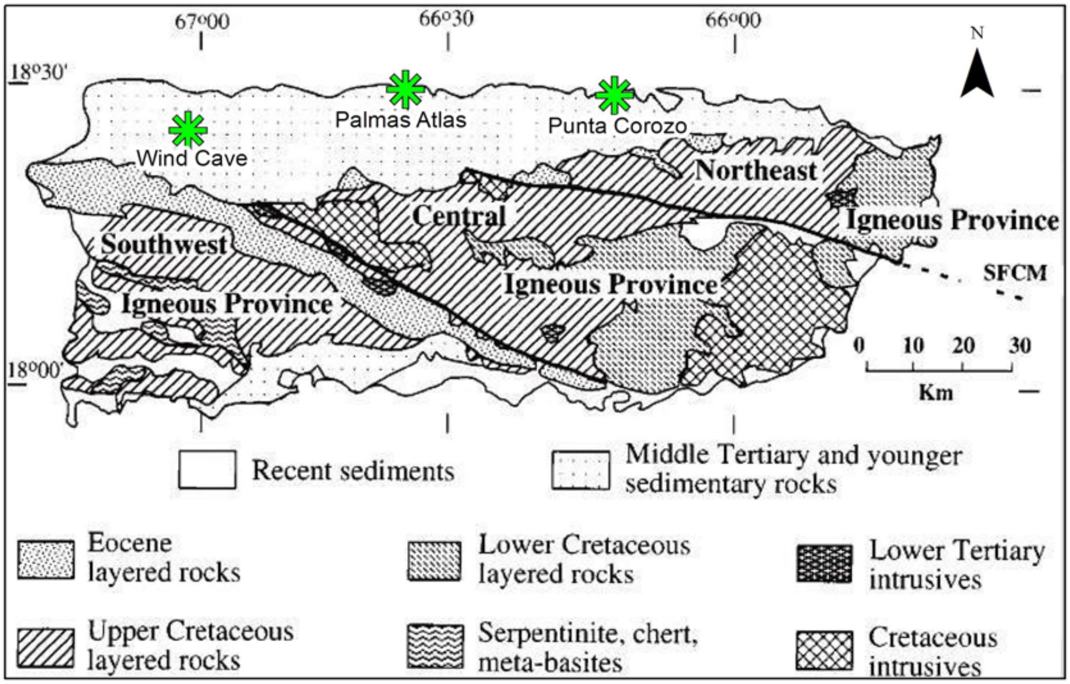


Figure 1. Geologic map of Puerto Rico with sampling locations (after Schellekens 1998). The white stippled area denotes carbonates. Coordinates for the sampling locations are Punta Corozo (Core 1: 18.4685, -66.199227; Core 2: 18.468141, -66.199017), Palmas Altas (Profile: 18.48393, -66.5756; Core: 18.484099, -66.574943), and the Cave of the Wind (18.417744, -66.967594). More detailed maps of the sampling locations are available from the authors.

input and potentially one of the leading sources of Caribbean soils (Muhs et al. 1990, 2007, 2009).

Modeling results suggest that during the last glacial period, fine-grained portions of Mississippi loess were carried by winds from the northwest and deposited thousands of kilometers away (Muhs et al. 2007). It is suggested that this loess may be a significant component of soils developed on the Florida Keys and the Bahamas, and a minor contributor to Barbados soils (Muhs and Budahn 2009). Prolonged volcanic activity in the Lesser Antilles island arc and volcanic ash from St. Vincent or Montserrant may also deposit a significant amount of nutrient rich material to the Puerto Rico mainland (Muhs et al. 2007; O'Farrill 2013).

Puerto Rico is comprised of large igneous rock provinces in addition to carbonates. This differs from previously studied Caribbean islands such as Barbados, where most of the island exposes reef-associated carbonate rocks (Vacher and Quinn 1997). Therefore another potential soil source may be derived from weathered rock material from the central mountains in the Northeast and Central Igneous Provinces of Puerto Rico (Fig. 1). Weathered material from high elevations could be transported down gradient and deposited in the carbonate regions of northern Puerto Rico.

Study Aims

The northern coastal plain of Puerto Rico is underlain by carbonate and siliciclastic rocks, which accumulated during Oligocene to

Pliocene time (Renken et al. 2002). This study focuses on soils formed on marine terraces along the northern coast of Puerto Rico. A marine terrace is a raised beach consisting of a shoreline that has been elevated above the wave-beach interface (Muhs et al. 2007). Marine terraces were selected because of their relatively pure composition of ~95% calcium carbonate, which allows for easier identification of outside sources and also may provide an age constraint if the exposure age is known (Muhs et al. 1990). The northern coast of Puerto Rico is home to an abundance of Cenozoic limestone that originated from a shallow-water carbonate platform setting (Taggart 1993). This study examines marine terraces at Palmas Altas and Punta Corozo, which were dated by ^{230}Th/^{234}U radiometric methods and have ages of 115-138 ka and 116-130 ka, respectively (Fig. 1; Taggart 1993). These ages are close to the Last Interglacial Maximum, which was characterized by dramatic sea level changes around 125 ka (Montoya 2007).

A secondary component of this project examines a carbonate speleothem specimen and associated soils collected from the Cave of the Wind in the Guajataca Commonwealth Forest, in northwestern Puerto Rico. Speleothems are good indicators of environmental changes due to their formational processes and have been extensively used for paleo-environmental reconstructions of continental areas (Frumkin and Stein 2004). Fine-grained particles trapped within speleothems or found in or above the cave should yield information regarding provenance.

METHODS

Soils on marine terraces were sampled at Punta Corozo and Palmas Altas (Fig. 1). Soils at Punta Corozo were sandier than Palmas Altas. Two soil cores were collected at Punta Corozo (PC1 and PC2) separated by approximately 20 m. Soil augers were used to core down until bedrock was reached. PC1 consists of seven samples taken along a depth of 56 cm; PC2 consists of six samples taken along a depth of 51 cm. After each auger head was filled with soil, it was removed and the soil sample was transferred into a labeled Ziploc bag. At Palmas Altas (PA), one 1.57 m soil core was collected and divided into 23 samples. In addition, 12 soil samples were collected from an exposed beach profile using a hand shovel. Soil samples from the Cave of the Wind were collected using a hand shovel above the entrance and at the back of the cave. A previously collected float speleothem and a rock sample from the path to the cave were also analyzed.

Soil samples were selected to represent the entire soil column. A subset of 30 samples were oven dried at 80°C until a constant mass was obtained, then heated at 1000°C in a muffle furnace to remove combustible components before trace and major element concentrations were determined by XRF (S4 Pioneer-Bruker) at Wesleyan University. A total of 12 samples from Punta Corozo and Palmas Altas were sent to SGS Mineral Services (Ontario, Canada) to obtain Th, Zr, Y, Ti and REE concentrations after fusion digestion and quantification by ICP-MS.

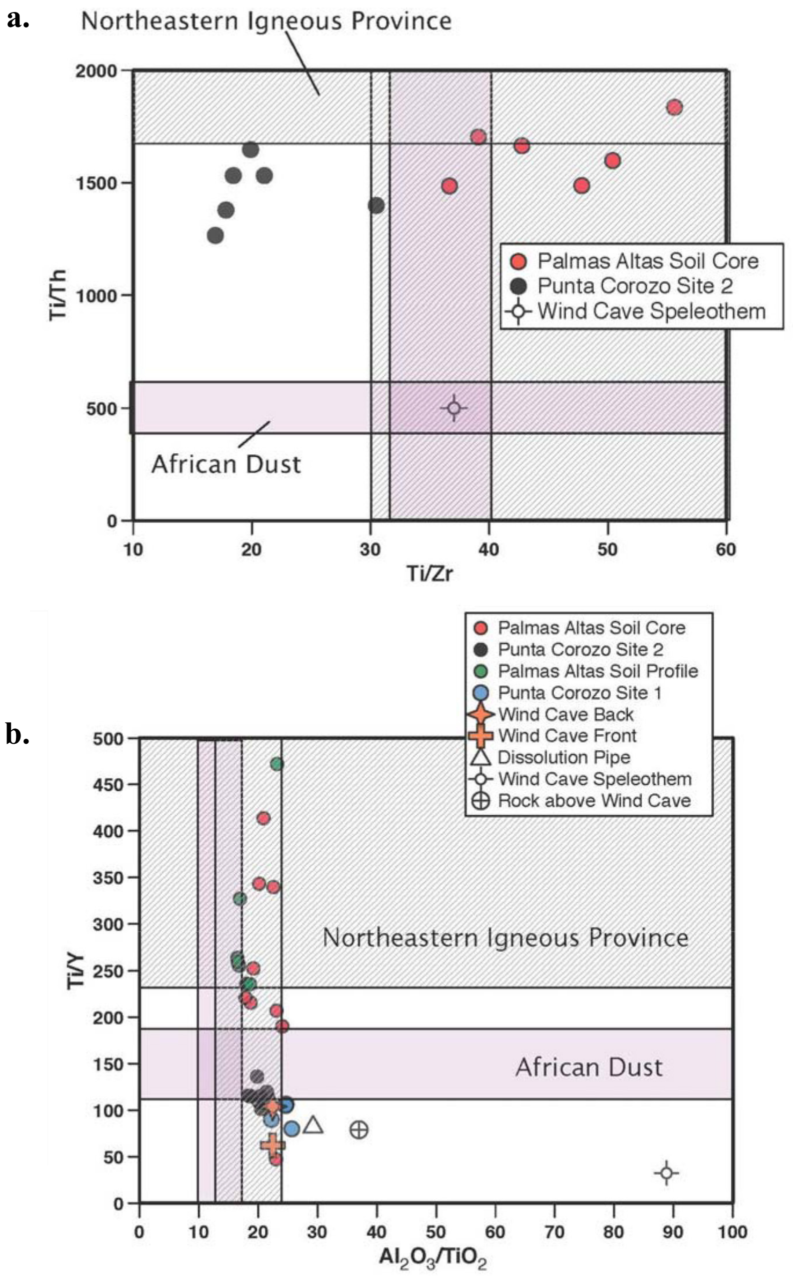
RESULTS

Characterizing Parent Materials Using Immobile Elements

Muhs et al. (1990) suggested that Caribbean volcanic ashes and Saharan dust can be identified by the difference in their immobile element ratios (Ti/Th, Ti/Zr, Ti/Y, Al_2O_3/TiO_2). The mean Al_2O_3/TiO_2 between Dominica ash and Saharan dust is significantly different, which makes this ratio useful for discriminating between Dominica volcanics and African dust. However, St. Vincent Al_2O_3/TiO_2 ratios overlap with those of Saharan dust, so Ti/Y, Ti/Zr, and

Ti/Th ratios were used to identify St. Vincent ash from African Dust. Our marine terrace data is compared to the Puerto Rican Northeastern Igneous Province and African dust in Fig. 2. For the Northeastern Igneous Province the field is represented by the average value (±1 standard deviation) from Schellekens (1998). The Ti/Th vs. Ti/Zr plot show that only the cave

Figure 2. a) Bivariate plot of Ti/Th vs. Ti/Zr; . b) Bivariate plot of Ti/Y vs. Al_2O_3/TiO_2. The pink area delineates the range of African dust; the shaded grey area delineates the northeastern igneous rocks (data from Schellekens 1998). The overlapping area of pink (or shaded) rectangles in each plot denotes the area that African dust (or igneous rock source) is most likely to be present.



speleothem sample falls into the overlapping African dust area (Fig. 2a). All Palmas Altas (PA) samples fall within the Northeastern Igneous Province region, with only two PA data points falling in the overlapping dust area. Five out of six Punta Corozo (PC) samples fall outside of both source regions.

On the Ti/Y vs. Al_2O_3/TiO_2 plot, five marine terrace samples fall into the African dust range for Ti/Y ratio, but none plot in the overlapping Al_2O_3/TiO_2 dust area (Fig. 2b). Both PA and PC samples have similar Al_2O_3/TiO_2 results. Most of PA and PC samples fall into the igneous rock range, and about 2/3 of the PA samples fall into the overlapping igneous rock area, suggesting a strong contribution from the Northeastern Igneous Province. The speleothem sample does not plot in any known field.

Discriminating Parent Materials Using Nd-Cr-Th and Zr-La-Sc Ternary Plots

Ternary diagrams of geochemically distinct elements are commonly used in provenance studies (Muhs et al. 2007). The Puerto Rican soils plot outside the fields representing African dust, Mississippi loess, and Dominica volcanics on a plot of Nd-Cr-Th, but do coincide with the northeastern and central igneous rocks (Fig. 3a). A few data points representing St. Vincent volcanics also overlap with the analyzed samples. On a Zr-La-Sc plot (Fig. 3b), the local igneous rock points slightly overlap with the African dust field, however most of the Puerto Rican soils fall outside of the African dust field, away from the St. Vincent and Dominica volcanics, and near the points from the Puerto Rican igneous provinces.

REE (Rare Earth Elements)

Eu/Eu* values may be applied to further characterize the source of soil parent material, where Eu is the chondrite normalized value of Europium and Eu* is the chondrite normalized value of Eu with respect to Sm and Gd values (Muhs and Budahn 2009). Higher Gd/Yb values indicate significant heavy REE depletion, a typical pattern for loess and other sediments derived from the upper continental crust (Muhs et al., 2009). An Eu/Eu* vs. Gd/Yb plot shows three possible sources. All of the Puerto Rican soil samples fall outside of the end-member values for African dust and Mississippi loess (shaded region), and are closer to the range of Caribbean volcanic sources (Fig. 4a). Chondrite normalized La/Yb ratios measure the relative amount of light REE to heavy REE (Muhs and Budahn 2009). The Sm/Yb vs. La/Yb plot (Fig. 4b) shows that while all Puerto Rican soil samples fall outside of the three end-member ranges, they are closer to the range of African dust and volcanic sources than Mississippi loess.

DISCUSSION

Muhs et al. (2007) suggested that soils on Barbados mainly develop from St. Vincent volcanic sources, with African dust as the secondary source. Soils developed on the Florida Keys and the Bahamas derive mostly from African dust and Mississippi loess. Because Puerto Rico is located in between these islands, it was hypothesized that an African dust signature could also be identified in soils from this study area. However, the bivariate and ternary plots (Figs. 2-3) suggest that igneous rock provinces in Puerto Rico are the major parent material for these marine terrace soils. The contribution of African dust, volcanic ash, and loess appears to be an insignificant contributor to parent material. An unpublished study by Dr. Daniel Muhs along the northern coast of Puerto Rico found similar results suggesting that the local bedrock mineral deposition rate is significantly higher than the African dust input rate. This explanation is applicable because Puerto Rico differs from the other nearby islands in that it consists of both limestone and igneous outcrops (Fig. 1), while

Figure 3. a) Ternary plot using Nd, Cr, and Th.; b) Ternary plot using Zr, La, and Sc (data from Muhs et al. 2007).

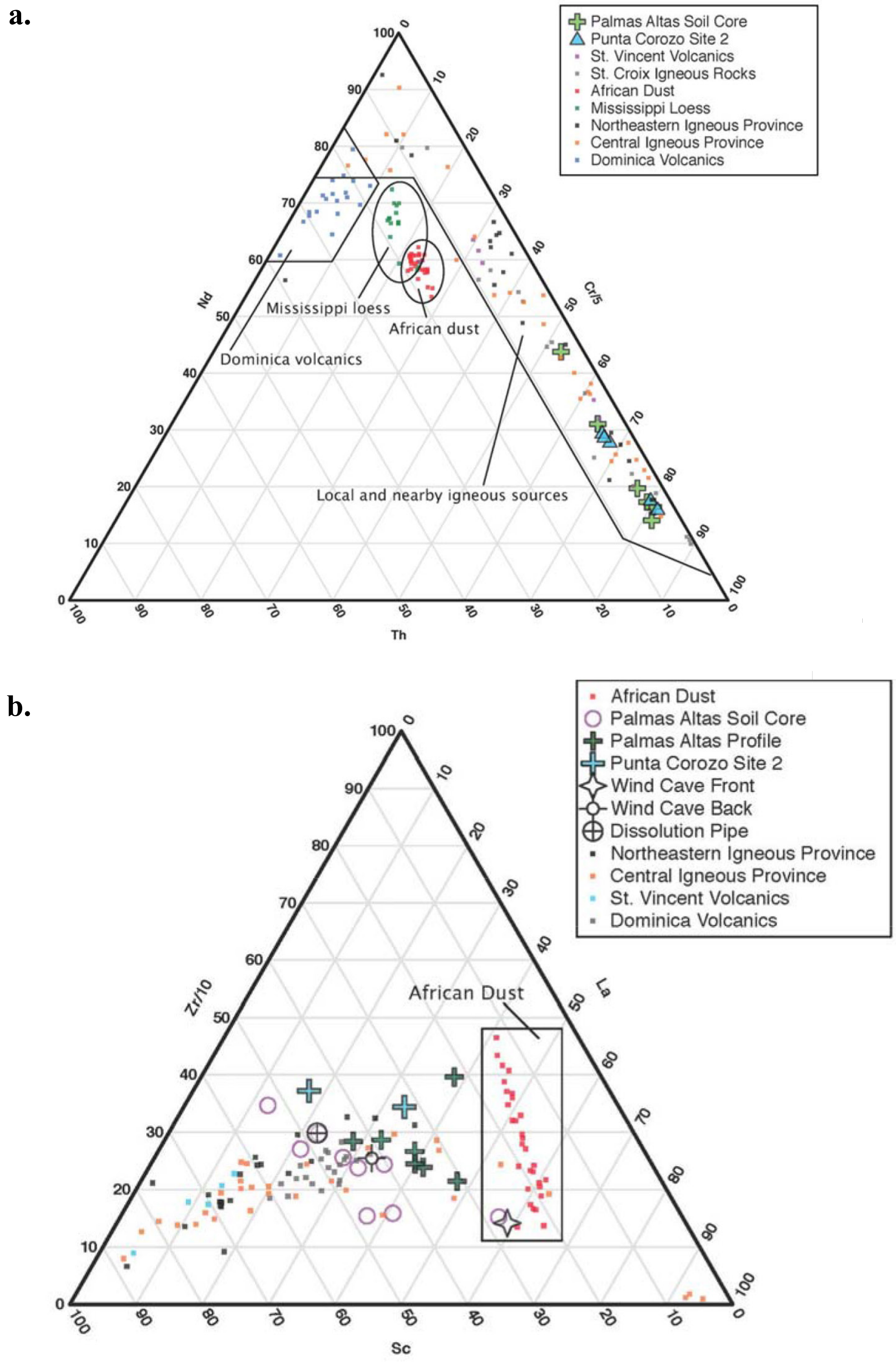
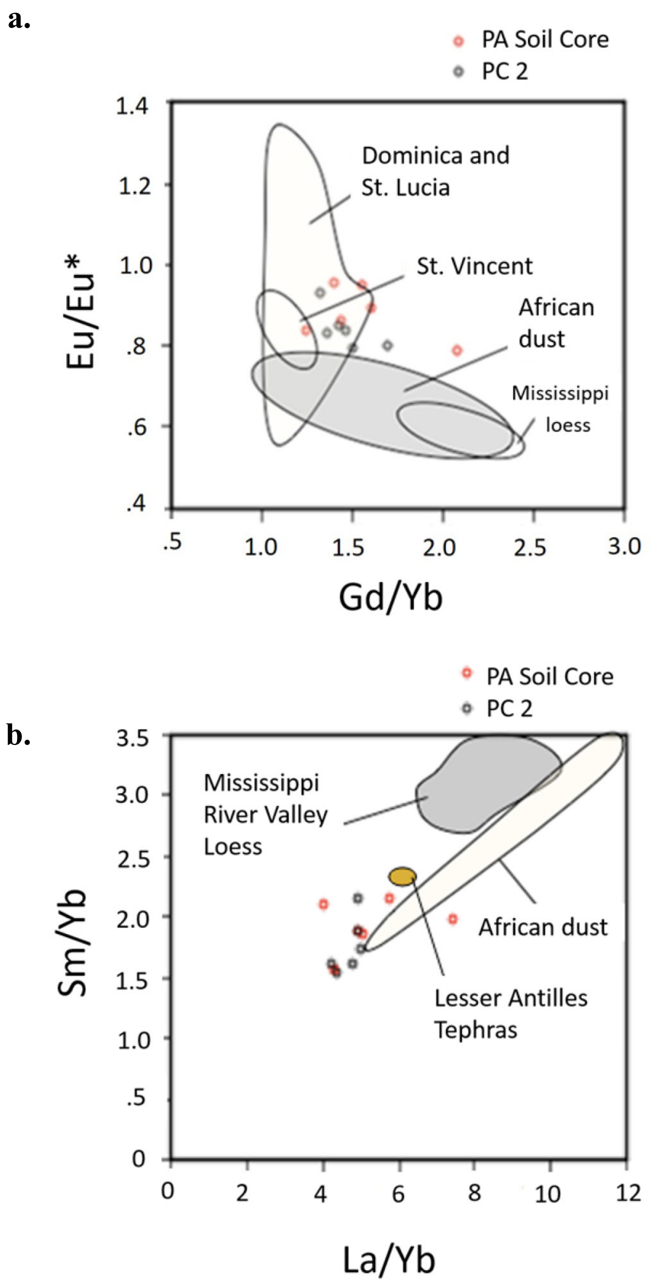


Figure 4. a) Eu anomaly for African dust, Dominica-St. Lucia volcanics, St. Vincent volcanics, and Mississippi loess (adapted from Muhs et al. 2007); b) Plot of Sm/Yb vs. La/Yb for African dust, Lesser Antilles tephras, and Mississippi loess (adapted from Muhs and Budahn 2009).



there is no major igneous rock formation on the previously studied islands such as the Florida Keys, Bahamas, and Barbados (Vacher and Quinn 1997). The absence of additional factors such as weathering of igneous rock material could also enhance the relative contribution of African dust in these study areas, further explaining the differences between island composition.

Both trace element and REE data were plotted against Muhs' 1990 and 2009 data for African dust and other end members. Rare element element data were unavailable for igneous rock end member. While Gd/Yb values fall within the range of African dust, elevated Eu/Eu* values suggest that volcanics from nearby Caribbean regions (or perhaps local volcanic rocks) are a more important source of Puerto Rican soils. Because of the proximity of data points to the region of African dust in Figure 4, we do not eliminate African dust as a contributing parent material in other parts of the Puerto Rican mainland. None of the sample points in Figure 4 fall near the Mississippi loess field, therefore loess is considered as an insignificant parent material. Additional REE data for the local igneous source would help to clarify these relationships.

The low sample numbers for the speleothem and cave soil samples yield inconclusive results. The analysis might also benefit from the utilization of strontium isotopes that have been used in previous studies to identify an African dust input in the speleothems (Frumkin and Stein 2004). In any case, more samples for both speleothem and soils around the cave will be needed to draw concrete conclusions as to their ability to record any dust signature in Puerto Rico.

CONCLUSION

Unlike other studies that have found distinct African dust signatures in Caribbean islands such as Barbados and the Bahamas, our trace element analysis indicates that local igneous rocks are the dominant parent material for soils developed on marine terraces in northern Puerto Rico. One possible explanation for these results is that the deposition rate of weathered local bedrock significantly outweighs dust deposition rates. Furthermore, marine terraces are situated within a high erosion area with constant wave action and may not be representative of productive inland soil. Differences in soil formation mechanisms may also be attributed to differences in island geology - Puerto Rico differs from previously studied Caribbean islands in that it has extensive igneous rock exposures in the central and southern portions of the island.

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HERBIVORY AND LEAF TRAITS IN *CECROPIA SCHREBERIANA* ALONG AN ELEVATION GRADIENT IN LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO

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ABSTRACT

The processes of leaf formation, function and senescence are inherently economic in nature and are well characterized by six leaf traits that comprise the worldwide leaf economic spectrum. This study examines leaves of *Cecropia schreberiana* along an elevation transect in the context of this spectrum. Leaves were sampled at four elevations in the Luquillo Experimental Forest, Puerto Rico, and analyzed for carbon content (C_{mass}), nitrogen content, and leaf mass per area (LMA), and the related economic variable: insect herbivory. Intraspecific correlations among leaf traits were weaker than established interspecific correlations, but the general patterns match. Elevation had a significant effect on C_{mass} and LMA but the patterns were not linear. Herbivory varied most strongly by elevation, perhaps in response to differing herbivore guilds.

Keywords: insect herbivory, *Cecropia schreberiana*, leaf economic spectrum, leaf mass per area, elevation gradient.

RESUMEN

Los procesos de formación, función y senescencia de las hojas se someten a una economía de recursos limitados, lo que se describe bien a través del rango de variación de seis rasgos funcionales, conocidos como el espectro global de economía foliar. Este estudio investiga las hojas de *Cecropia schreberiana* a lo largo de un transecto de elevación en el contexto de este espectro. Se tomaron muestras en cuatro puntos de elevación en el Bosque Experimental de Luquillo/ Bosque Nacional El Yunque, Puerto Rico y se analizaron el contenido de carbono, el contenido de nitrógeno y la masa foliar por área (MFA), con respeto a la variable económica relevante: la herbivoría de insectos. Las correlaciones intraespecíficas entre rasgos de hojas fueron más débiles que las correlaciones interespecíficas establecidas, pero las tendencias generales son compatibles entre sí. Se encontró un efecto significativo de la elevación en el contenido de carbono y la MFA, pero el efecto no era lineal. La herbivoría varió de manera más fuerte en correspondencia con la elevación, quizás como respuesta del gremio de herbívoros.

Palabras clave: herbivoría por insectos, *Cecropia schreberiana*, espectro económico foliar, masa/área foliar, gradiente elevacional.

INTRODUCTION

Although leaves largely share the same basic functions of photosynthesis and transpiration, globally they exhibit an enormous range of traits. These physical and chemical traits embody different investments of resources in order to maximize photosynthetic yield or minimize water loss over time, representing strategic trade-offs inherently economic in nature. Wright et al. (2004) assembled data on key chemical, structural and physiological properties of leaves around the world through a global leaf-monitoring network. The data describe a universal spectrum of co-varying leaf traits: the worldwide leaf economic spectrum. At one end of the spectrum are “fast-return” leaves with high nutrient concentrations, high rates of photosynthesis and respiration, short leaf lifespans and low leaf dry mass per area (LMA). On the other end of the spectrum are more expensive, “slow-return” leaves, characterized by long lifespans, high LMA, low nutrient concentrations, and low rates of photosynthesis and respiration.

Numerous follow-up studies have both corroborated the leaf economic spectrum worldwide and explored various extensions and applications (Wright et al. 2005b, Shipley et al. 2006, Westoby and Wright 2006, Santiago 2007, Royer 2008, Chave et al. 2009). Here we investigate several factors related to the leaf economic spectrum but less well-established: intraspecific variation, elevation gradients, and co-variation with herbivory.

The leaf economic spectrum focuses on variations in leaf traits across thousands of species, but intraspecific variation is understudied. Intuitively, intraspecific variation should follow similar patterns as interspecific variation, however scale can fundamentally alter ecological processes and patterns (Levine 2000, Sandel and Smith 2009).

Implicit in the leaf economic spectrum is the idea that certain leaf traits are well-adapted to specific environments. Interest in the response of leaf traits to climate has blossomed (Wright et al. 2005a). Doria et al. (2010) investigated phenotypic plasticity of leaf traits along an elevation gradient in *Cecropia schreberiana* in the Luquillo Experimental Forest (LEF) also known as El Yunque National Forest. With increasing elevation, they found a decrease in leaf area ($r^2 = 0.28$) and C/N ratios ($r^2 = 0.94$), and a corresponding increase in leaf mass per area (LMA, $r^2 = 0.95$) and area-based nitrogen content (N_{area}, g/m^2; $r^2 = 0.91$). They posited that changes in leaf morphology were a result of harsher environmental conditions at higher elevations, requiring plants to invest more resources to produce sturdier leaves. High winds, cooler temperatures, lower photosynthetically active radiation levels, and high relative humidity leading to the formation of water films on leaves all make the production of high LMA leaves with low nutrient concentrations and low photosynthetic rates more economical, fitting the trend of the leaf economic spectrum, with “cheaper” leaves at lower elevations and more “expensive” leaves at higher elevations (Doria et al. 2010).

Insect herbivory on leaves is interrelated with many of the traits characterized by the leaf economic spectrum. More expensive leaves generally have higher LMA and higher concentrations of lignins, which make feeding by insects more difficult physically (Coley et al. 1985, Coley 1988). Expensive leaves also tend to have higher concentrations of tannins, secondary bitter compounds (Coley 1988). These traits generally decrease herbivory, but require additional investment of resources (Strauss et al. 2002, Kempel et al. 2011). Thus, using the leaf economic spectrum framework, we predict that relative herbivory correlates positively with nitrogen concentration by mass (N_{mass}) and negatively with LMA (Coley 1983, Kudo 2003).

Here we further explore and expand on leaf trait patterns in *C. schreberiana* in the LEF. We address three primary questions focused on exploring the leaf economic spectrum: Does intraspecific variation in leaf traits follow the same patterns established on a global scale by the leaf economic spectrum? How does elevation affect leaf traits in *C. schreberiana*? And how does variation in leaf traits affect herbivory? We hypothesize that: 1) intraspecific variation will follow patterns established by Wright et al. (2004); 2) at higher elevations there will be a shift to higher LMA and lower N_{mass} leaves; and 3) leaves with lower N_{mass} and higher LMA will experience less herbivory.

METHODS

Cecropia schreberiana is a fast-growing tree with very weak, light (and initially, hollow) wood, and a 30 to 50 year lifespan. *Cecropia schreberiana* plays a key role as a pioneer species in the LEF, facilitating rapid succession and the ultimate development of a mature forest after disturbance. It is one of few species that can be found in most forest types in the LEF. *Cecropia schreberiana* trees are most abundant at mid-elevations in the tabonuco forest, moderately abundant in the palo colorado and palm forests, and rare or absent in the dwarf forests (Brokaw 1998).

In January 2012, we sampled leaves at four sites within the LEF: at 330 meters above sea level at the base of the Bisley canopy tower; at 400 m along route 9966 near the site of a recent landslide and near the intersection with route 191; at 721 m in the Mt. Britton trailhead parking lot; and at 923 m near the top of Mt. Britton. These sites are close (but not identical) to those visited in 2008 by Doria et al. (2010). At each site we collected two to four leaves from each of three mature *C. schreberiana* trees (minimum dbh of 10 cm, 12 trees total) using a pole pruner. We preferentially sampled the older, outer leaves to standardize for leaf age; older leaves typically accumulate more insect herbivory (Myster 2002). In the field, the leaves were labeled, photographed, wrapped in newspaper and placed in plant presses for transport. At Wesleyan, leaves were put in a drying oven for at least 7 days. Each leaf was weighed twice, at least one week apart, to ensure leaves were dry. Subsamples were taken with a paper hole puncher from the largest (central) lobe, near the tip, avoiding leaf veins and areas of herbivory. For very thin leaves, two or more holes were punched. Hole punches were wrapped in tared tin foil cups and weighed. N_{mass} and C_{mass} were determined using a Thermo Finnigan Flash 1112 Series Elemental Analyzer, using aspartic acid and L-cysteine as standards.

Each leaf image was manipulated with Adobe Photoshop such that holes and edges (when edges were clearly missing due to herbivory) were reconstructed and saved as a layer in Adobe Photoshop. Images were then analyzed using ImageJ for the following three area measurements: 1) leaf area: area of intact leaf (original, pre-photoshopping area); 2) pre-herbivory area: intact leaf area + area missing due to herbivory; 3) herbivory area: area missing due to herbivory (including area of non-penetrating herbivory). The quantity of herbivory was calculated using the formula: % herbivory = (herbivory area / pre-herbivory area)*100. Leaf mass per area was calculated as leaf mass / intact leaf area.

Data were analyzed in R. Percent herbivory was modeled using a linear mixed effects model (nlme package) with elevation, N_{mass}, C_{mass} and LMA as fixed factors and nested by tree. We included explanatory variables in the model based on our hypotheses and excluded rainfall and LMA interactions based on AIC scores. The AIC scores were consistently lower for models including tree as a random factor. In addition, variables were excluded to avoid co-linearity among explanatory variables and so that there was sufficient replication for an analysis. For example we used the N_{mass} instead of N_{area} because N_{area} is highly correlated with LMA (Fig. 1) partially because both have units with area in the denominator. The C/N was also correlated with LMA and was excluded. Herbivory by site and leaf traits was then compared by ANOVA. The ANOVA satisfied both assumptions of normality and homoscedasticity. Multiple independent ANOVAs were conducted with elevation as the dependent variable, N_{mass}, N_{area}, C_{mass}, C/N, and LMA as response varia-bles, and the leaves nested by tree. Leaf mass area and N_{area} were log transformed. The residuals of each ANOVA passed a Shapiro-Wilk test of normality. To correct for the increased type 1 error rate inherent in multiple testing, the Dunn-Šidák solution was used. With five ANOVAs, this reduced the significance level to p = 0.01.

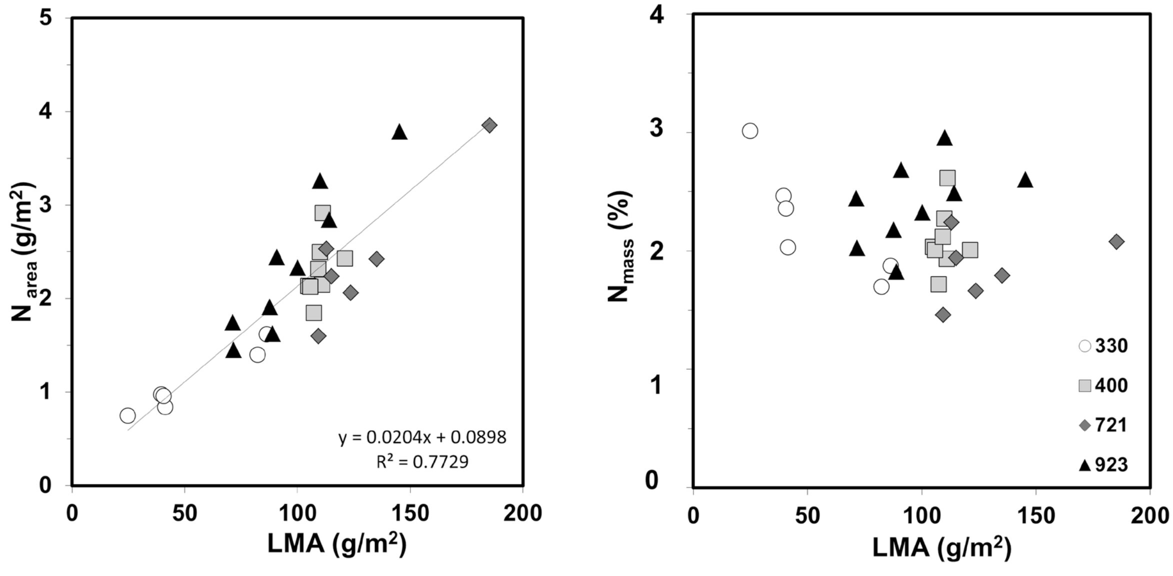
RESULTS

Leaf mass area and N_{area} are strongly positively correlated within *C. schreberiana*, while N_{mass} and LMA are very weakly negatively correlated (y = -0.0029x + 2.45, r^2 =0.07). Among all leaves sampled, N_{area} ranged from 0.75 to 3.85 g/m^2 (mean = 2.10 g/m^2), N_{mass} ranged from 1.28 to 3.01 % (mean = 2.15 %), and LMA ranged from 24.73 to 185.32 g/m^2 (mean = 98.47 g/m^2).

In the context of the global leaf economic spectrum, *C. schreberiana* falls near the middle. Globally, LMA ranges from 14 to 1,500 g/m^2 and N_{mass} ranges from 0.2 to 6.4% (Wright et al. 2004). With a mean LMA of 98.47 g/m^2 and mean N_{mass} of 2.15 %, *C. schreberiana* leaves are near the center of the range but leaning towards the faster, cheaper end of the spectrum. This fits the role of a fast-growing pioneer species, while still being a perennial tree.

The leaf traits all varied with elevation, although the differences are significant only for

FIGURE 1. N_{mass} versus LMA (left) and N_{area} versus LMA (right) among all leaves. Each point represents an individual leaf (n = 29). Leaves are grouped by elevation (meters asl).



C_{mass} and LMA (Table 1; Fig. 2). Rather than the expected linear trends with elevation, the relationships are mostly unimodal: N_{area}, C_{mass}, LMA and C/N peak at mid-elevations, while N_{mass} dips at mid-elevations (Fig. 2).

Patterns of herbivory are largely driven by elevation, but N_{mass} and C_{mass} also had a significant effect (Table 2; Fig. 3). No interactions terms were significant.

DISCUSSION

Intraspecific variation in *C. schreberiana* broadly follows the interspecific patterns reported by Wright et al. (2004). Here, LMA is strongly positively correlated with N_{area} and negatively correlated with N_{mass} (Fig. 1), matching the global, interspecific relationships. The correlation, however, between LMA and N_{mass} is extremely weak ($r^2 = 0.06$), while that between N_{area} and LMA is very strong ($r^2 = 0.77$). Globally, N_{mass} is more tightly correlated to LMA than N_{area} ($r^2 = 0.34$ and 0.57, respectively, reported on a log-log scale) and is more commonly used as a leaf economic variable (Wright et al. 2004). Moreover, LMA and N_{area} are both measured on an area basis, so their correlation is partly an artifact of shared denominators. If leaves from the highest elevation are excluded, the correlation between LMA and N_{mass} improves considerably ($r^2 = 0.24$, or 0.30 on a log-log scale) and better matches global patterns; the anomalous behavior of the highest-elevation site is discussed later.

A comparison of leaves sampled here with those of Doria et al. (2010) shows similar trends by elevation, although our values of LMA, N_{mass}, and N_{area} are consistently lower at a given elevation. The cause of this discrepancy is unknown but could be due to interannual variation in environmental conditions (seasonal variation is not considered because both studies sampled in January).

In contrast to our study, Doria et al. (2010) found a strong increase in N_{area} with elevation. The authors posited that harsher conditions at higher elevations induced construction of more expensive, durable leaves (Doria et al. 2010). Here, N_{area} levels off at the highest elevation, displaying a hump-shaped relationship (Fig. 2). Considering this hump-shaped distribution is found consistently across the leaf traits measured, including the core leaf economic traits LMA, N_{area} and N_{mass}, the Doria et al. (2010) hypothesis of cheap leaves at low elevation and expensive leaves at high elevation is weakened.

Generally, an increase in elevation corresponds to a smooth change in climate (e.g., temperature, rainfall); wind speed is different, increasing sharply near the summit. Previous work in the LEF showed that high wind-exposure near the mountain summits causes stunted growth and altered physiology in *C. schreberiana*. Individuals protected from wind at the summit had lower N_{mass} than exposed trees (Cordero 1999). Here, individuals at the summit had a higher N_{mass} than expected based on the other sites, which could be driven by high winds at the summit. If the highest elevation site is excluded, patterns across the other three sites are consistent with that from Doria et al. (2010).

Community assembly theory posits that shifts in trait distributions along environmental gradients are driven by species turnover with intraspecific plasticity playing a smaller role (Cornwell and Ackerly 2009). Although we do not have data on community level traits along our elevation gradient, the trait plasticity in *C. schreberiana* shows some role for intraspecific variation. Naturally, however, the trait ranges shown by *C. schreberiana* are much smaller than the range of all leaves globally, and the correlations among traits are weaker and slopes of change are shallower than the global economic spectrum.

Table 1. Summary of statistics of multiple independent ANOVAs on leaf trait variation by site.

Variable	**df** (numerator/denominator)	**F**	**p**
N_{mass} (wt %)	3/8	3.62	0.0648
C_{mass} (wt %)	3/8	8.04	**0.0085**
N_{area} (g/m^2)	3/8	6.05	0.0187
C/N (molar ratio)	3/8	7.09	0.0122
LMA (g/m^2)	3/8	9.57	**0.0050**

bold p-values are significant ($p<0.01$, using the Dunn-Šidák correction)

Figure 2. N_{area} (top left), herbivory (top right), N_{mass} (bottom left) and LMA (bottom right) versus elevation. Points represent sample means of individual leaves (at 330 m n = 6 for LMA, herbivory, and N_{area}, n = 8 for N_{mass}; at 400 m n = 8 for LMA, herbivory, and N_{area}, n = 9 for N_{mass}; at 721 m n = 6 for LMA, herbivory, and N_{area}, n = 9 for N_{mass}; at 923m n = 9 for LMA, herbivory, N_{area}, and N_{mass}). Error bars show one standard deviation.

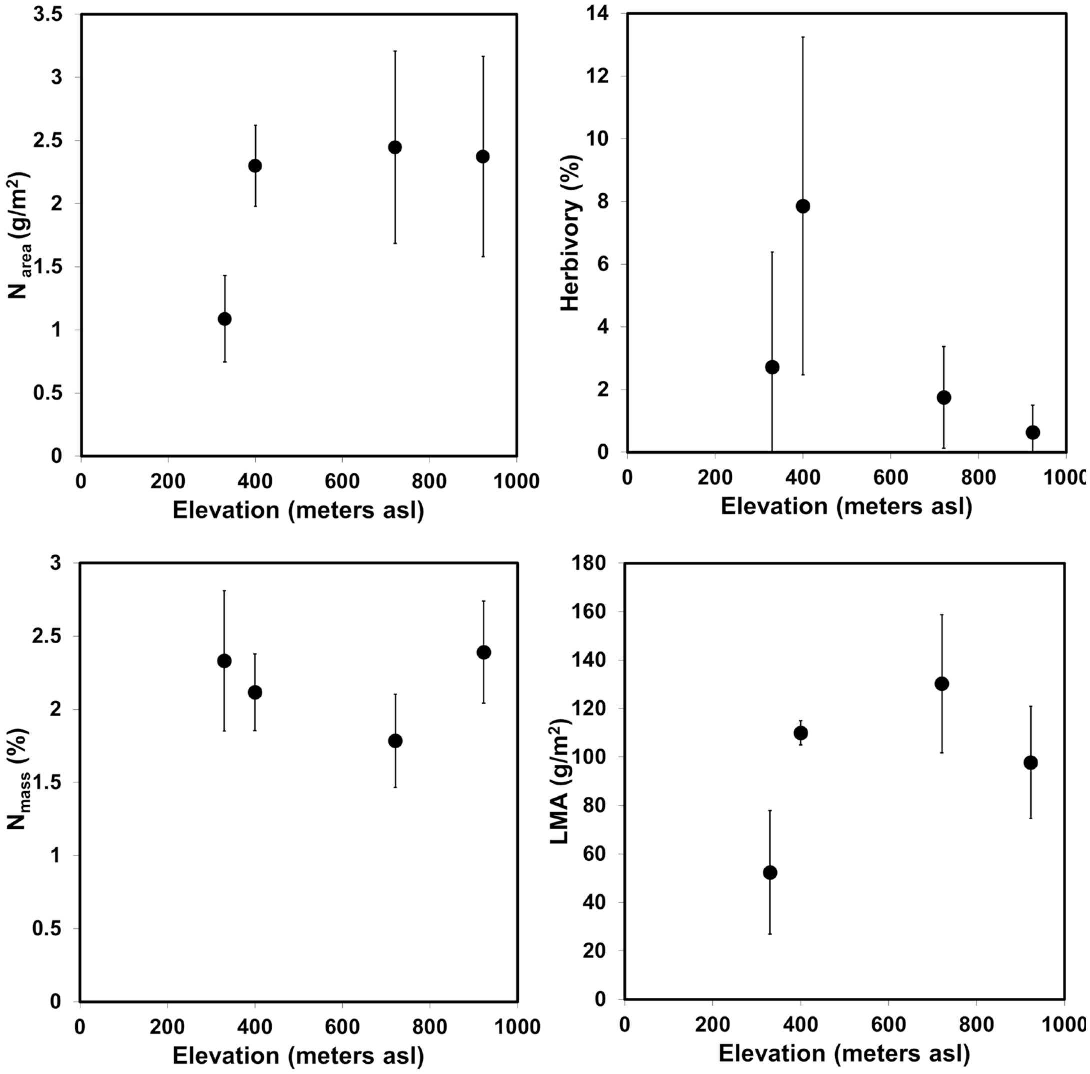
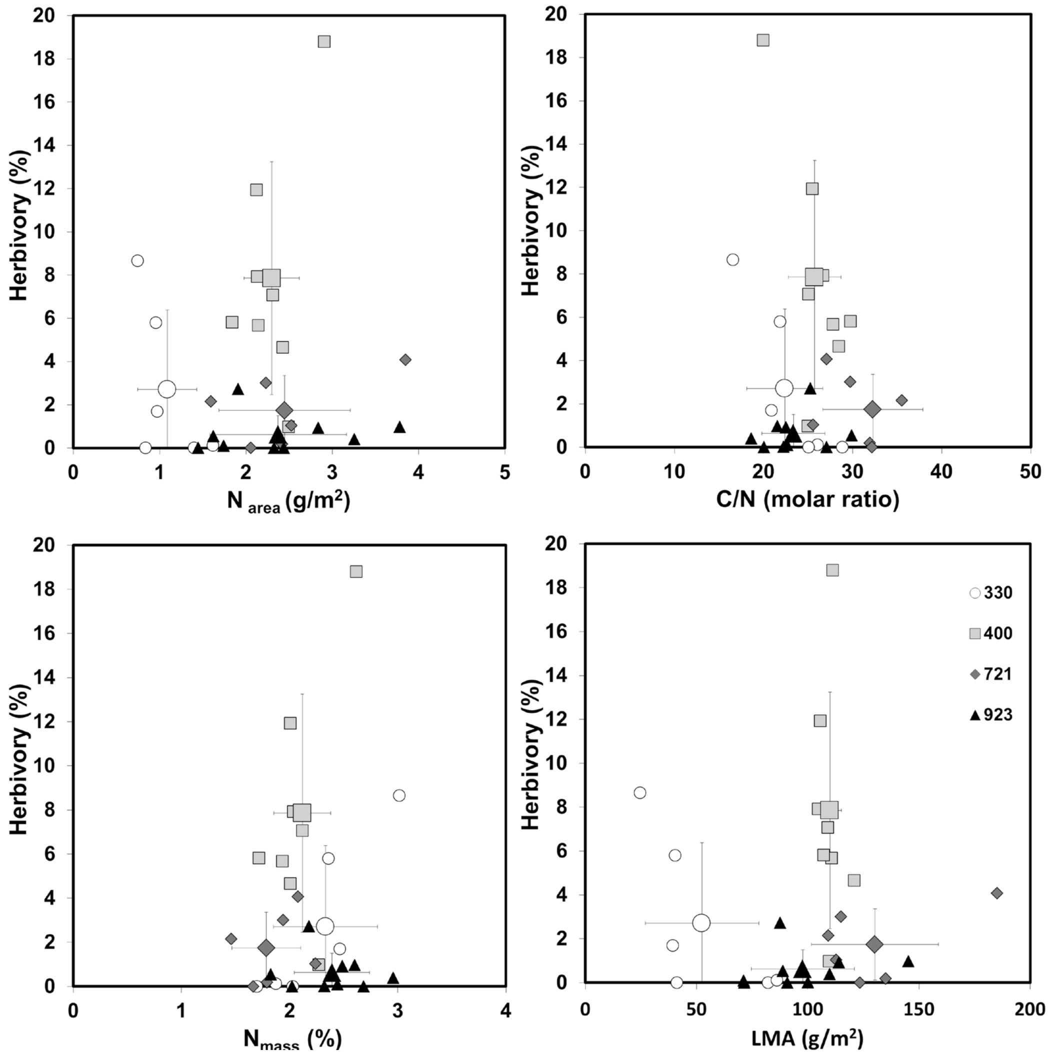


TABLE 2. Summary of ANOVA statistics on percent herbivory damage to leaves.

Variable	**df** (numerator/denominator)	**F**	**p**
Elevation	3/8	27.29	**0.0001**
N_{mass} *(wt % N)*	1/4	20.17	**0.0109**
C_{mass} *(wt % C)*	1/4	17.37	**0.0141**
LMA (g/m^2)	1/4	0.39	0.5639
Elevation$\times N_{mass}$	3/4	6.45	0.0518
Elevation$\times C_{mass}$	3/4	5.25	0.0714
$N_{mass}\times C_{mass}$	1/4	3.86	0.1207
Elevation$\times N_{mass}\times C_{mass}$	3/4	2.45	0.2030

× denotes interactions; **bold p-values** are significant ($p<0.05$).

FIGURE 3. Comparison of herbivory versus N_{area} (top left), C/N (top right), N_{mass} (bottom left) and LMA (bottom right). Individual leaves are shown by the smaller points and grouped by elevation (meters asl). The larger points represent the means for each elevation, with the error bar representing one standard deviation.



Change in herbivory was driven primarily by elevation, although some leaf traits did have a significant effect (Table 2). Higher N_{mass} was associated with higher herbivory, which corroborates previous findings that herbivores feed preferentially on nutritious, N-rich leaves (Coley 1983). Higher C_{mass} was also positively correlated with higher herbivory, although the effect size was much smaller. Initially this was surprising because C_{mass} is often correlated with C/N ratios, which are used as a measure of leaf toughness and have been negatively correlated to herbivory rates (Craine et al. 2003, Xiang and Chen 2004). Here, however, C_{mass} and C/N were very weakly negatively correlated (r^2=0.05). Still, C/N ratios were not included in the herbivory model due to co-linearity with LMA (r^2 = 0.15). Just using elevation and C/N in the same model, however, shows that C/N has a significant negative effect on herbivory (p=0.02), supporting the hypothesis that herbivores are deterred by tough leaves. A direct comparison of C/N to herbivory shows little correlation (Fig. 3). Without the high elevation site however, there is a stronger negative correlation between C/N and herbivory (r^2 increases from 0.05 to 0.24).

Although we expected herbivory to be driven primarily by leaf traits, not elevation, ecological theory also posits that herbivore assemblages and herbivore pressure vary along complex environmental gradients and help structure plant communities (Louda 1982, 1989). Herbivory does not vary monotonically along the elevation gradient here, but distinct forest types were seen at each sampling site. Therefore, herbivory on *C. schreberiana* may be driven by variation in the surrounding plant community and corresponding insect assemblages.

CONCLUSION

Intraspecific variation of leaf economic traits in *C. schreberiana* leaves matched the global interspecific patterns, albeit more weakly. We hypothesized that variation in environmental conditions along an elevation gradient would underpin this variation, with cheaper leaves at lower elevations and expensive leaves at higher elevations. Although there was significant variation in leaf traits by elevation, the relationships were not linear. This contrasts with previous findings (Doria et al. 2010) and could not be explained adequately with our data, although it is potentially related to unusual environmental conditions in the LEF. Further investigation quantifying environmental conditions throughout the forest and looking at community-level leaf traits may identify stronger patterns and illuminate the ultimate drivers of variation in leaf traits in the LEF.

As hypothesized, high N leaves experienced higher herbivory. However the effect of N was eclipsed by herbivory differences among the sites, likely due to different insect guilds at each locale. Future work with controlled feeding studies and identifying specific herbivore presence and frequency at different elevations may help disentangle these factors.

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PRODUCTIVITY INDICES FROM LEAF CHEMISTRY: A STUDY OF POLLUTION EFFECTS IN PUERTO RICAN *RHIZOPHORA MANGLE*

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ABSTRACT

Mangrove forests are highly productive and important carbon sinks, but their response to nitrogen loading is not well characterized. Here we use leaf chemistry to explore the source and effects of nitrogen inputs to two mangrove ecosystems in northeastern Puerto Rico: a relatively non-polluted site in the protected Ceiba Commonwealth Forest near Los Machos and a polluted site near the mouth of the Fajardo River in an urban setting 5 km downstream from an active waste treatment plant. Weight percent and stable isotopic composition of leaf carbon and nitrogen were used to quantify anthropogenic nitrogen loading and to model forest productivity. Results reveal both increased nitrogen loading and productivity at the polluted Fajardo site relative to the Los Machos site. These data can inform mangrove ecosystem protection efforts and guide wastewater management strategies.

Keywords: mangroves, pollution, productivity, leaf chemistry, carbon, nitrogen.

RESUMEN

Bosques de manglares son sumideros de carbono muy productivos e importantes, pero su respuesta a la carga de nitrógeno no está bien caracterizada. Aquí, usamos química de la hoja para explorar la fuente y los efectos de la aportación del nitrógeno en dos ecosistemas de manglar en el noreste de Puerto Rico: un sitio relativamente no contaminado en el Bosque Estatal de Ceiba protegido cerca Los Machos y un sitio contaminado cerca de la desembocadura del Río Fajardo en un sitio urbano localizado 5 km aguas abajo de una planta de tratamiento de aguas residuales. Se midió el porcentaje en peso y la composición isotópica estable del carbono y nitrógeno en las hojas con el fin de cuantificar la carga de nitrógeno y poder modelar la productividad forestal. Resultados revelan tanto el aumento de la carga de nitrógeno y la productividad en el sitio contaminado en el Río Fajardo con relación al sitio estudiado en Los Machos. Esta data puede ayudar a informar los esfuerzos de protección de los ecosistemas de manglar y la gestión de las aguas residuales.

Palabras clave: manglares, contaminación, productividad, química foliar, carbono, nitrógeno.

INTRODUCTION

Mangroves comprise extremely productive and unique forest ecosystems at the junction of land and sea. Compared to other woody species, mangroves maximize their water use efficiency through phenotypic plasticity in response to environmental changes (Alongi 2002). In order to support high productivity rates, mangroves grow extensive root networks. As a result, mangrove ecosystems are very important carbon sinks; on a global scale, mangrove forests store more carbon than other ecosystems, especially in their soils: whole tropical ecosystem carbon pools of mangrove forests average 956 Mg C ha^{-1} versus 241 Mg C ha^{-1} for moist forests and 593 Mg C ha^{-1} for salt marshes (Alongi 2014).

Mangrove systems are generally characterized by relatively simple food webs, but act as refuges for many species. Their extensive canopy cover creates a sheltered nursery ground and breeding site for coastal fish, crustaceans, birds, reptiles, and some mammals. Also, the steady accumulation of sediment in mangrove areas helps to protect against coastal erosion and floods. As a result, mangrove forests are key protectors against increasing threats of sea level rise and increased erosion rates as a result of global climate change (Alongi 2002).

In Puerto Rico, mangrove forests occupy 8,323 ha of land and sea, providing essential benefits for species, coastal landscapes, and carbon sequestration (Martinuzzi et al. 2009). Our study focuses on the red mangrove (*Rhizophora mangle*) in northeastern Puerto Rico. We seek to investigate the effects of pollution, particularly anthropogenic nitrogen inputs, on the productivity of *Rhizophora mangle*.

Previous studies have explored the link between nitrogen loading and productivity in mangroves (e.g., Fry and Cormier 2011), with leaf chemistry analyses used to identify coastal watershed inputs based on mangrove productivity levels. Fry and Cormier's study (2011) reveals higher degrees of nitrogen and phosphorus limitation in rural mangrove forests and in urban mangroves with limited freshwater inputs. Feller et al. (2003) examined the effects of nutrient inputs on *Rhizophora mangle*, focusing on disturbed mangrove ecosystems. Although they did not observe productivity directly, their results indicate increased growth rates in response to nitrogen fertilization (Feller et al. 2003). Other studies note the ability of mangroves to serve as sinks for anthropogenic and industrial pollutants (Maiti and Chowdhury 2013). Mangrove systems contain sediment with a high sorptive capacity; excess nutrients in mangrove sediment can also be important for boosting the productivity of the ecosystem (Giblin et al. 1980).

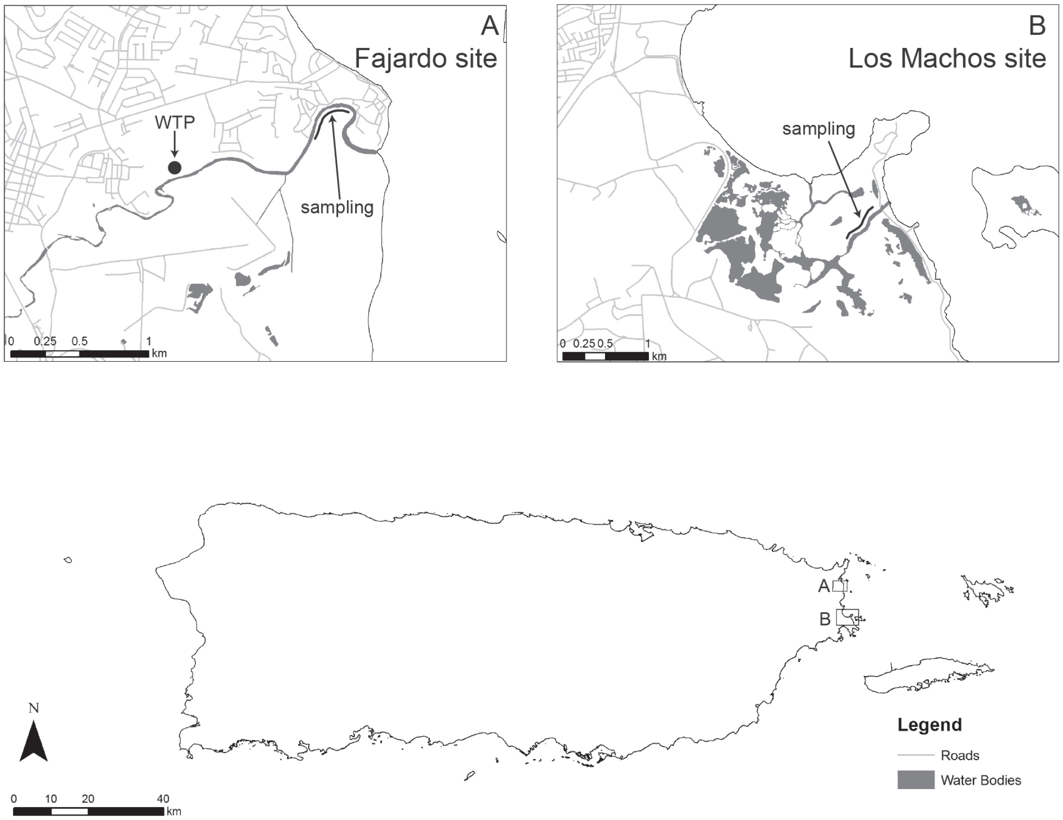
We hope to build on these studies by comparing a polluted site to a nearby less polluted site. In particular, we seek to test whether nitrogen loading affects site productivity. We hypothesize that mangroves at the polluted site are more productive due to nutrient loading.

METHODS

We gathered red mangrove leaf samples from two sites in northeastern Puerto Rico: an urban mangrove forest near the mouth of the Fajardo River ~5 km downstream from a wastewater treatment plant ('Fajardo' site) and 1 km downstream from an abandoned wastewater facility; and a protected site in the wetlands of Ceiba State Forest at Los Machos ('Los Machos' site) (Fig. 1). At each site, 100 leaf samples were collected by kayak from 10 trees. All sampling took place on a single day (January 13, 2015) and leaves were immediately labeled, pressed, and dried.

For lab analysis, leaves in the best condition were favored. Forty (40) composite samples

Figure 1. Map of sampling areas. Black labeled lines demarcate the boundaries of our sampling (leaves were sampled from both sides of each water channel). An old wastewater treatment plant is marked ("WTP"). The active Fajardo Regional Wastewater Treatment Plant is ~5 km upriver from our sampling at the Fajardo site. Map made in ARC GIS using data from http://gis.pr.gov.



were used for chemical analyses: a hole punch was used to commingle leaf tissue from four leaves per composite sample. Sampling location within each leaf was standardized to reduce potential intra-leaf variation in chemistry. Samples were weighed and wrapped in tin. All analyses were contracted to the University of California Davis Stable Isotope Facility.

MODES OF ANALYSIS

$\delta^{15}N$ in mangrove leaves can act as a tracer of nitrogen sources because different nitrogen sources have isotopically distinct nitrogen values (Kendall and McDonnell 1998). In plants, higher values of $\delta^{15}N$ often indicate anthropogenic inputs from activities such as agriculture or wastewater runoff. In general, animal waste (including human waste) is elevated in $\delta^{15}N$ due to trophic scaling (Kendall and McDonnell 1998). The primary reason for high $\delta^{15}N$ values in regions affected by anthropogenic discharge is the partial denitrification of nitrate from agricultural fertilizers, manure, or sewage entering the water supply upstream (Fry and Cormier 2011). The $\delta^{15}N$ from plants that take up nitrate converted from animal wastes generally range from +10‰ to +20‰ compared to -5‰ to +2‰ for plants without these nitrogen sources (Kendall and McDonnell 1998).

While the link between $\delta^{15}N$ enrichment and wastewater and agricultural runoff is well established, it is possible to find no effect, for example if there is rapid freshwater runoff that does not allow for microbes to denitrify, or if shoreline waters are diluted by tidal mixing with offshore waters. In these cases, nitrogen content may be a better tracer for nitrogen sources than $\delta^{15}N$; thus, it is important to measure both (Fry and Cormier 2011).

To estimate the relative productivities of mangroves at our two sites, we adopted the productivity model of Fry and Cormier (2011) based on Hawaiian mangroves. In this model, productivity scales with the product of leaf $\delta^{13}C$ and weight percent nitrogen. Leaf nitrogen content reflects nutrient supply to the plant, while $\delta^{13}C$ is related to the demand/supply function that governs the balance of CO_2 uptake and water loss. Thus, relative productivity in this model is defined as (demand/supply) × supply.

C:N ratios indicate the degree of nitrogen limitation. A high C:N value within a single species may signify a nitrogen deficiency while a low ratio may be related to nitrogen loading.

RESULTS

$\delta^{15}N$ values are higher at the polluted Fajardo site than at Los Machos, with a 14‰ difference in the means (Fig. 2). The Fajardo mangroves also have a lower C:N ratio than at Los Machos, indicating a greater access to nitrogen. The productivity index is higher at the Fajardo site, with a mean value of 45 versus 24 at Los Machos (Fig. 2).

A two-way ANOVA test was performed for leaf samples, with site and within-site samples as the two factors (Table 1). This was done to test the significance of values both between and within sites. The results for $\delta^{13}C$ and $\delta^{15}N$ show significant

Figure 2. Mean carbon and nitrogen isotopic values (‰), C:N mass ratio, and calculated productivity (*$\delta^{13}C$ × weight percent nitrogen*) measured at each site. Bars are standard errors of the mean. FR = Fajardo River site (more polluted); LM = Los Machos site (less polluted).

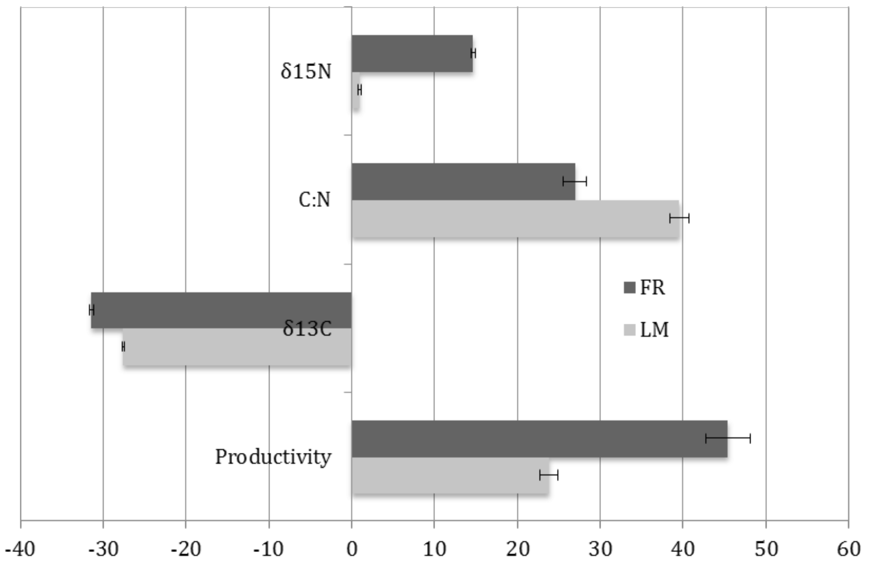


Table 1. *p*-values for two-way ANOVA test for the factors site and within-site samples.

	Site	**Sample**
$\delta^{13}C$	0.02	0.01
$\delta^{15}N$	0.01	0.04
C:N	0.05	0.12
Productivity	0.04	0.06

differences both within and across sites; for C:N and productivity, there are significant differences across sites, but not within. There is no covariance for any variable, meaning site variance does not affect the sample variance.

DISCUSSION

We see increased nutrient loading and productivity levels at the polluted Fajardo site, supporting our initial hypothesis (Fig. 2). We attribute the high $\delta^{15}N$ values at Fajardo to two wastewater treatment plants upstream (one active, one abandoned; Fig. 1). The mean $\delta^{15}N$ value of 15‰ is in the range for sewage and manure runoff (+10‰ to +20‰; Kendall and McDonnell 1998). In contrast, the mean value of +1‰ at Los Machos is in the range for non-polluted nitrogen sources (-5‰ to +2‰; Kendall and McDonnell 1998).

The productivity model of Fry and Cormier (2011) suggests a higher productivity at Fajardo (Fig. 2), which we attribute to increased nitrogen loading. The lower C:N ratio at Fajardo (27 vs. 39 at Los Machos) is also consistent with nitrogen loading. The baseline of McKee (1995) suggests that a C:N ratio of <18 is representative of red mangroves growing in nutrient enriched environments, while a ratio of >37 represents low nutrient enrichment. Our results are consistent with a sharp difference in nutrient availability between the two sites.

CONCLUSIONS

Mangrove forests provide essential physical and biological support for coastal ecosystems, and can serve as an important carbon sink. Therefore, our study can inform conservation efforts. Anthropogenic nutrient loading has strongly affected the mangrove ecosystem at the Fajardo River site. Although elevated productivity at Fajardo is probably linked with an increased capacity for carbon sequestration, continued nitrogen inputs may ultimately become harmful due to eutrophication and the formation of dead zones (Rivera-Monroy et al. 2004). Therefore, instances of increased productivity due to anthropogenic nutrient loading are warning signs of future ecosystem stress.

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EFFECT OF POLLUTION ON SEAGRASS ECOSYSTEMS IN GUÁNICA BAY AND CABO ROJO, PUERTO RICO

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ABSTRACT

Seagrass meadows are productive shallow water marine environments that perform vital ecological functions globally. Despite their importance, seagrass beds are declining more rapidly than nearly any other marine environment due to increased human disturbance like pollution, habitat destruction, sedimentation, and physical trampling. We compare coverage, height, species composition, and leaf chemistry of a seagrass bed at the eastern mouth of Guánica Bay with a bed in Cabo Rojo to determine whether the Guánica Bay site is significantly degraded by pollution. Guánica Bay is a populated area subjected to sewage, agricultural runoff, and industrial heavy metal contamination, while Cabo Rojo is located in an isolated bay within a coastal preserve. We find that the carbon and nitrogen isotope values in seagrass leaf tissue at Guánica Bay are indistinguishable from that at Cabo Rojo. Therefore, isotope ratios in Guánica Bay seagrass tissue do not reflect elevated sewage and industrial runoff compared to Cabo Rojo. We found statistically significant variations in species composition, percent cover, and overall productivity between the two sites, and we suggest that these differences may reflect environmental factors such as water depth, wave action, and human recreation, but do not appear to reflect coastal nutrient pollution.

Keywords: Seagrass, coastal pollution, marine ecology.

RESUMEN

Los prados de hierba marina son ambientes productivos de agua marina poco profunda que realizan funciones ecológicas vitales a nivel mundial. A pesar de su importancia, los prados de hierba marina están disminuyendo más rápidamente que casi cualquier otro ambiente marino debido al aumento de las perturbaciones humanas como la contaminación, la destrucción del hábitat, la sedimentación y pisoteo físico. Comparamos la cobertura, la altura, la composición de especies y la química de las hojas de un lecho de vegetación marina en la desembocadura oriental de la Bahía de Guánica con un lecho en Cabo Rojo para determinar si el sitio de la Bahía de Guánica se degrada significativamente por contaminación. La Bahía de Guánica es un área poblada sometida a la aguas residuales, la escorrentía agrícola y contaminación de metales pesados por la industria, mientras que Cabo Rojo está situado en una bahía aislada dentro de una preserva costera. Encontramos que los valores de los isótopos de carbono y nitrógeno en el tejido de las hojas de hierbas marinas en la bahía de Guánica son indistinguibles con los de Cabo Rojo. Por lo tanto, las proporciones de isótopos en el tejido de las hierbas marinas en la Bahía de Guánica no reflejan aguas residuales o desechos industriales elevados en comparación con Cabo Rojo. Encontramos variaciones estadísticamente significativas en la composición de las especies, el porcentaje de cobertura y la productividad global entre los dos sitios, y se sugiere que estas diferencias pueden reflejar factores ambientales como la profundidad del agua, la acción del oleaje y la recreación humana, pero no parecen reflejar la contaminación de nutrientes costeros.

Palabras clave: hierbas marinas, contaminación costera, ecología marina.

INTRODUCTION

Seagrass meadows are ranked among the most productive marine environments and are important to coastal and marine ecosystems around the globe (Cullen-Unsworth and Unsworth 2013). These ecosystems contain seagrasses (marine flowering plants) and usually occur in shallow, tropical, and coastal waters where there is enough sunlight to penetrate to the sediment (Mcleod et al. 2011). Seagrass meadows provide numerous ecosystem services that are essential to environmental and human wellbeing, including carbon sequestration, organism habitat and biodiversity, sediment stabilization, and organic carbon production. However, seagrass habitats are experiencing destruction rates greater than or equal to those of tropical forests, mangroves, salt marshes, and coral reefs (Cullen-Unsworth et al. 2013). Seagrass communities are sensitive to anthropogenic effects; they have thus been deemed "coastal canaries" (Orth et al. 2006).

Biomass, productivity, density, and distribution of seagrasses are important parameters for managing seagrass beds (Wilson and Dunton 2012). Percent cover estimation is a method used to analyze species composition in sample plots quantitatively, and can demonstrate the specific conditions preferred by different species (Wilson and Dunton 2012). Disturbed seagrass beds are often comprised of opportunistic species such as *Syringodium filiforme*, while undisturbed areas typically contain climax species like *Thalassia testudinum* (Di Carlo and Kenworthy 2008). The overall cover and species composition of seagrasses have therefore been used to identify areas of potential effects and degradation, and we measured these indicators in our present study (Fig. 1; Whitall et al. 2012; Wilson and Dunton 2012).

Canopy height can determine the structural role of seagrass beds in an ecosystem. Taller seagrasses have a higher potential for providing complex habitat structures and protection for epifaunal organisms. Additionally, canopy height is directly related to sedimentation rates (Table 1; García et al. 1999) and can be compared between different species, making it an important meadow descriptor (Duarte and Kirkman 2001).

Nitrogen isotope ratios ($\delta^{15}N$) of seagrass leaf tissue vary depending on nutrient sources and can link seagrass beds to pollution sources (Costanzo et al. 2001). $\delta^{15}N$ values in unpolluted *Thalassia* most frequently lie between 0‰ and +8‰, but can vary from −2‰ (McClelland et al. 1997) to +12.3‰ (Fourqurean et al. 2005) depending on the seagrass ecosystem (Anderson and Fourqurean, 2003; Lepoint et al. 2004). $\delta^{15}N$ values close to 0‰ are attributed to N_2 fixation by healthy seagrass organisms (Yamamuro et al. 2003). Higher values (+5 to +10‰) generally indicate the influx of manure or sewage effluent (Lepoint et al. 2004).

Figure 1. Box charts comparing A) total percent cover, B) canopy height, C) percent *Thalassia*, and D) percent *Syringodium*. The bottom and upper "whisker" of each plot denote the lower and upper non-outlier extremes, respectively, and the bottom and upper edges of each box denote the lower (25th) quartile and upper (75th) quartile, respectively. The thick lines in the middle of each plot denote the median. Dots outside of the box-and-whisker plot denote outliers.

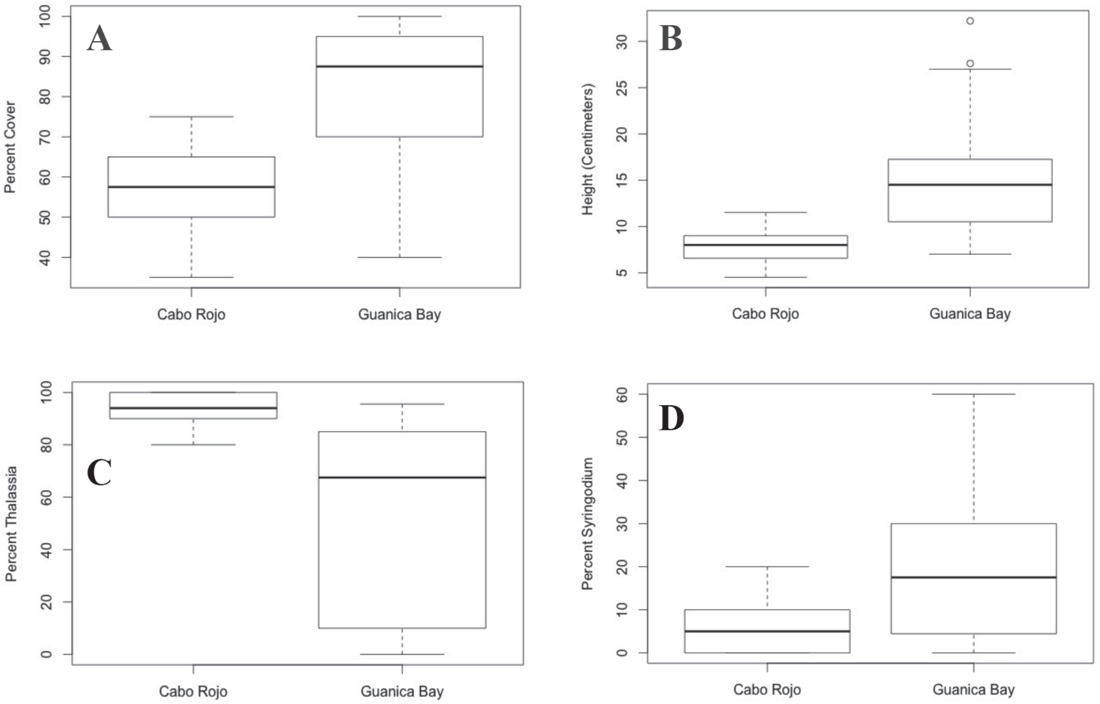


Table 1. Seagrass health indicators and the services that they represent (after García et al. 1999).

Indicator	Significance
Species composition	Different seagrass species reflect different environmental conditions and successional stages.
Percent cover	Seagrass ecosystem services like productivity, fish habitat health, and sedimentation correlate positively with percent cover.
$\delta^{13}C$ and $\delta^{15}N$	These ratios vary between nutrient sources and implicate potential pollution sources such as sewage or agriculture
Canopy height	Can indicate habitat viability for juvenile fishes, often correlates with water depth.

Seagrasses are C_3 plants, but *T. testudinum* can metabolize bicarbonate and/or CO_2 directly from the water column through different photosynthetic pathways (Anderson and Fourqurean 2003). The type of photosynthetic pathway utilized is reflected in the carbon isotope ratio ($\delta^{13}C$). For healthy *Thalassia* tissue, values most commonly range between -10‰ and -11‰, but can fall within -24‰ to -3‰ (Hemminga and Mateo 1996). Lower ratios can reflect a sewage effluent influx, which contains a lower $\delta^{13}C$ than atmospheric or marine sources (Hemminga and Matteo 1996).

In our present study, we measured major chemical and physical indicators of seagrass ecosystem health and pollution, including species composition, percent cover, canopy height, and carbon and nitrogen stable isotope compositions in seagrass leaf tissue. Our goal was to assess and compare the contemporary levels of pollution and disturbance at two seagrass sites (Fig. 2): one that was located quite near to Guánica Bay, which is known to contain high levels of pollution (Whitall et al. 2014), and another within the Cabo Rojo recreational and marine park, which is isolated from most anthropogenic runoff. The construction of five agricultural reservoirs in the Guánica Bay watershed has expanded the watershed five-fold to its current size of 400 km^2 by changing local topographies and altering drainage capacities. This change increased the supply of clay, nutrient, and other pollution inputs to Guánica Bay (Rodríguez 2013). However, it is unclear whether seagrasses located at the Guánica Commonwealth Forest, just east of the Bay's mouth, are as heavily degraded as well-documented seagrass communities within Guánica Bay (Whitall et al. 2014). We accessed the site via the protected Guánica Commonwealth Forest, at an access point off PR-33 just southeast of the mouth of Guánica Bay (Fig. 2). In contrast to the Guánica site, the Cabo Rojo Peninsula seagrass beds are relatively pristine. The site was accessed from La Playuela, a beach within the Cabo Rojo protected area. This beach is located at a small inlet at the Southern tip of the Cabo Rojo península (Fig. 2).

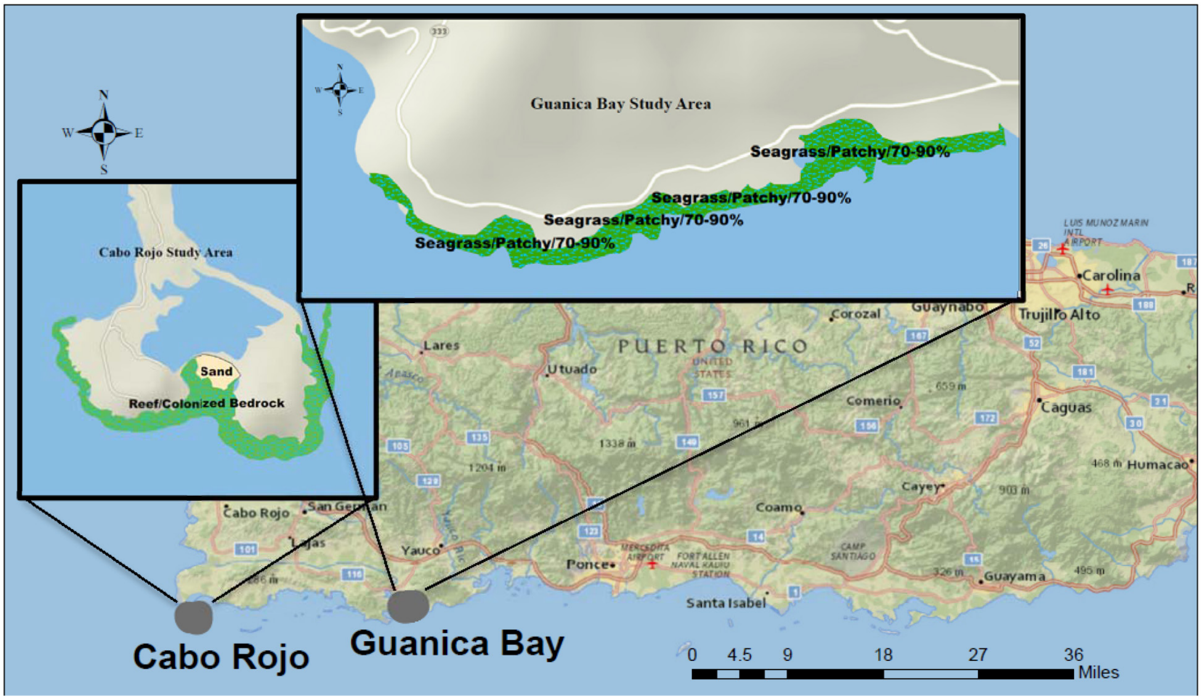
METHODS

At each site, two 30 m tapes were deployed to establish parallel transect lines. Weights or stakes secured the transect tape at either end, with additional stakes placed along the transect line to stabilize the measuring line. One square meter PVC quadrat was placed at every five meter point along these transect lines, yielding six sampling sites.

Species composition and total percent cover of each quadrat were estimated using the Braun-Blanquet scale. Canopy height was measured following Duarte and Kirkman (2001). In each quadrat we grabbed a handful of rooted plants and gently pulled them to their maximum height without uprooting. Measurements from the sediment to the top fifth of the plant were recorded. Additionally, water depth was measured in each quadrat to normalize for canopy height. To account for tides, fieldwork was conducted between early morning and early afternoon at both sites on consecutive days.

We took leaf samples by laying a yardstick horizontally across each quadrat and sampling every intersecting leaf. We measured the length and width of all sampled leaves. In the lab, leaves were washed with vinegar and scraped clean to remove epiphytes and excess organisms. Next, leaves were dried in an oven at 75 °C and ground to a fine powder using a mortar and pestle. Leaf powder was then shipped to the Stable Isotope Facility at University of California, Davis for $\delta^{13}C$ and $\delta^{15}N$ ratio analysis.

Figure 2. Map of Puerto Rico with locations of non-pristine (Guánica Bay; right inset) and pristine (Cabo Rojo; left inset) sites. Seagrass is shown in green (Whitall et al. 2014).



Data were analyzed using several statistical techniques. This included t-tests to test for statistically significant differences between the two sites and a correlation matrix table to aid in examining the magnitude and direction of the bivariate relationships between our measured variables. To test the statistical significance of percentages, we first applied an angular transformation in order to create normal distributions.

RESULTS

A substantial difference was found in the total percent cover between the two sites, with Cabo Rojo averaging 57.5% total cover and Guánica Bay averaging 80.5% (Fig. 1A; $t_{26} = -4.41$, $P < 0.001$). There is also a statistically significant difference in seagrass bed height at Cabo Rojo (average ~8 mm) and outside of Guánica Bay (average ~16 mm) (Fig. 1B; $t_{21} = -4.24$, $P < 0.001$).

A substantial difference was found in percent *Thalassia* (relative to all seagrass cover) (Fig. 1C) and percent *Syringodium* (relative to all seagrass cover) (Fig. 1D) between the two sites. Cabo Rojo averages 94% *Thalassia* and 6% *Syringodium*, while Guánica Bay averages 55% *Thalassia* and 20% *Syringodium*. A t-test revealed that the differences are statistically significant at the 99% and 95% confidence levels, respectively, for *Thalassia* and *Syringodium* ($t_{24} = 4.73$, $P < 0.001$; $t_{28} = -2.57$, $P = 0.02$).

A negative correlation between percent *Thalassia* and percent *Syringodium* (-0.19, P = 0.33) indicate that an increase in one will lead to a proportional decrease in the other. A negative correlation between percent *Thalassia* and total percent cover (-0.42, P = 0.02) indicates that an increase in *Thalassia* is accompanied by a decrease in total percent cover and vice-versa. We also see a positive relationship between percent *Syringodium* and total percent cover (0.61, $P < 0.001$), a weak negative relationship between percent *Thalassia* and canopy height (-0.08, $P = 0.68$), a positive relationship between canopy height and total percent cover (0.46, $P = 0.01$), and a positive relationship between percent *Syringodium* and canopy height (0.59, $P < 0.001$) (Table 2).

The 20 *Thalassia* leaf tissue samples from Cabo Rojo produce an average $\delta^{13}C$ of -9.50‰ and $\delta^{15}N$ of +1.70‰, while the 16 *Thalassia* samples from Guánica produce an average $\delta^{13}C$ of -9.69‰ and $\delta^{15}N$ of +1.80‰ (Fig. 3). Neither of the between-site differences are statistically significant ($\delta^{13}C$: $t_{36} = 0.29$, $P = 0.77$; $\delta^{15}N$: $t_{36} = 0.61$, $P = 0.55$). These values are within the range for healthy seagrass beds that receive nutrients from unpolluted sources.

DISCUSSION

Percent Cover and Canopy Height

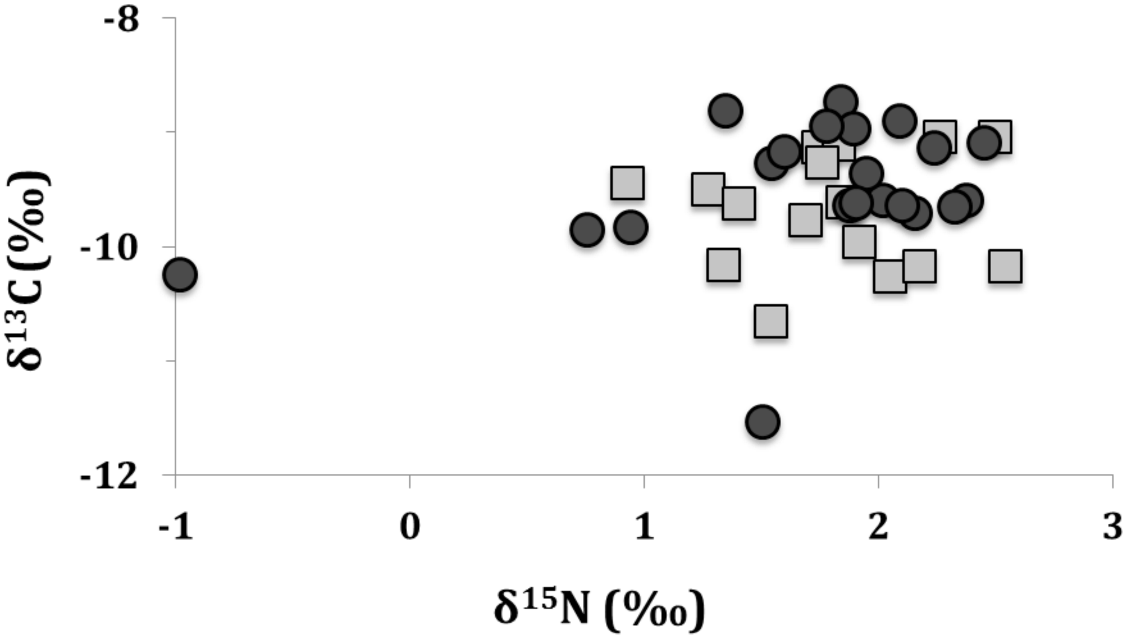
We find lower cover of seagrass at Cabo Rojo than at Guánica Bay (see Fig. 1A). Ruiz and Romero (2003) found an association between seagrass cover reduction and increased physical disturbance, and we argue that our values show potential physical disturbance at the Cabo Rojo site. While the relatively remote beach does not host boating activity, we encountered more powerful waves and more recreational swimmers wading in and around the seagrass beds, but we did not quantify these factors in this present study. Eckrich (1998) identified a relationship between increased trampling and reduced seagrass cover. Given that the Cabo Rojo site is more popular among recreational beachgoers than the Guánica Bay site, an increase in wading and trampling may explain differences in cover between our two sites, especially because *Syringodium* is a hardier pioneer species that does better in disturbed environments (Eckrich 1998).

Canopy height has an important role in seagrass structural complexity and resulting ecological dynamics. Mean seagrass canopy height was shorter at Cabo Rojo than at Guánica Bay (Fig. 1B). We consider that this difference is mainly due to *Thalassia* being inherently shorter than *Syringodium*. Some seagrass species like *Thalassia* have more biomass in their complex root systems than in aboveground foliage; this structurally complex seagrass root network provides a habitat for infaunal organisms (Di Carlo and Kenworthy 2008). Although the canopy height is shorter at Cabo Rojo, the *Thalassia* root network may be more established. Taller canopy height has been linked to increased sedimentation rates; this may suggest that sediment is more easily trapped at Guánica Bay than at Cabo Rojo, where wave action is much stronger (García et al. 1999).

TABLE 2. Correlation matrix for select seagrass health indicators.

	Canopy height	***Thalassia***	***Syringodium***
Percent cover	0.46, P = 0.01	-0.42, P = 0.02	0.61, P < 0.001
Canopy height		-0.08, P = 0.68	0.59, P < 0.001
Thalassia			-0.19, P = 0.33

Figure 3. δ^{13}C and δ^{15}N results for *Thalassia* from both seagrass bed sites. Each data point represents the δ^{13}C:δ^{15}N ratio for individual leaf tissue samples from Cabo Rojo (dark circles) and Guánica Bay (light squares).



The differing physical conditions between the sites may be partially responsible for the differences in percent cover and canopy height. In addition to increased trampling disturbance at the Cabo Rojo site, the current is much stronger and the waves were much more pronounced than at Guánica Bay. The substrate is rockier at Cabo Rojo, which may not support a seagrass meadow with high percent cover and tall blades. The seagrass meadows are also in relatively deeper waters at Cabo Rojo; with more suspended sediment from wave and current activity, the amount of available light might be limited.

Seagrass Species Composition

Gallegos et al. (1994) showed that *Syringodium* can fulfill the role of pioneer species during succession of seagrass beds after disturbance. This species rapidly grows tall stalks in high densities, but is relatively short-lived and inefficient at nutrient recycling compared to a climax species like *Thalassia*. *Syringodium* can serve as an intermediate meadow species between the algal colonization and reestablishment phases of a climax community; this would make it an optimal species to occupy a meadow following a turbidity event or physical disturbance (Williams 1990; Di Carlo and Kenworthy 2008). In general, *Syringodium* can invade spaces at a much faster rate than *Thalassia* (Gallegos et al. 1994).

One particular point of interest is the relatively high nutrient requirement of *Syringodium*. This high nutrient requirement could suggest that this species established itself at Guánica following a period of nutrient addition. Gallegos et al. (1994) postulated that Caribbean meadows of *Syringodium* are typically replaced by *Thalassia* as the community develops. Our results suggest that while Cabo Rojo seems more disturbed than Guánica Bay based on canopy height and percent cover, the species composition is characteristic of a climax community. Climax seagrass communities vary greatly from one another in terms of canopy height and percent cover, but species composition is closely related to these variables because *Syringodium* tends to have higher canopy height (Di Carlo and Kenworthy 2008). Seagrass communities sampled near Guánica Bay may therefore be in the midst of an ecological replacement process that began in recent decades after major modifications were made to Guánica Bay.

Di Carlo and Kenworthy (2008) suggested that the colonization of Puerto Rican seagrass beds may not follow a simple path of succession (e.g., algae to *Syringodium* to *Thalassia*), but that seagrass species may have relatively equal opportunities to colonize. In this case, successful colonization would depend on the local conditions of the meadow and the requirements of the competing species. As physical conditions change to favor less-disturbed communities, replacement of other species with *Thalassia* may become more common. Furthermore, the definition of climax communities has been challenged in recent reports. Williams (1990) suggests that climax communities can contain multiple species that occupy different niches (in the case of seagrasses, different levels of habitat) and are each limited by a certain resource. Through this lens, both of our sites may be relatively stable communities with different resource concentrations or physical conditions. Physical conditions were different between the sites, and these differences may favor certain seagrass species more than others, resulting in the variance between our sites.

Nutrient supplies and $\delta^{13}C$ and $\delta^{15}N$

Leaf tissue analyses from both sites produce indistinguishable carbon and nitrogen isotope ratios. These values are all within the range of unpolluted seagrass beds. The seagrass beds growing at the mouth of Guánica Bay therefore appear to be relatively uninfluenced by contemporary anthropogenic nutrient pollution. However, similar stable isotope ratios across both sites do not eliminate the possibility that previous disturbance could have caused an ecological shift at the Guánica Bay site, which may be responsible for the significant differences in species composition.

CONCLUSIONS

We analyzed seagrass communities in two areas: Cabo Rojo, a relatively pristine and isolated site, and Guánica Bay, which is located near industrial facilities and was assumed to be relatively polluted and degraded. Although seagrass meadows at Guánica Bay were in close proximity to effluent sources, they are isotopically similar to the seagrasses in Cabo Rojo. Meadows at the mouth of Guánica Bay may not be severely affected by chemical and sediment pollution, both well-documented within Guánica Bay, but further studies, perhaps investigating sediment core records, are required to address the validity and possible causes of this conclusion. Although Cabo Rojo is relatively far from industry and pollution sources, canopy height and percent cover were lower than at Guánica Bay. This can be attributed to a number of factors, including increased disturbance from recreational activities and abiotic conditions such as increased wave action and rocky substrates.

Contrary to our initial hypotheses, both sites exhibit modern day characteristics of good health, and we found no evidence that the Guánica Bay site is currently degraded by industrial or municipal pollution that is well-documented in Guánica Bay. We demonstrate that although the protected Guánica Bay site is located quite near to the mouth of a heavily polluted bay, this protected marine area still houses functioning and diverse seagrass communities. It is important to consider these issues when conducting environmental impact assessment and remediation during development projects.

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HEAVY METAL ACCUMULATION IN *BRASSICA JUNCEA* GROWN ON PUERTO RICAN SERPENTINE SOIL

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ABSTRACT

Serpentine soils are characterized by high concentrations of the trace metals Ni, Co, Cr, Mn, Cu, and Zn, making them a useful proxy for studying anthropogenically contaminated soils. To explore the potential for plants to remediate soils contaminated with metals, we grow *Brassica juncea* in controlled growth chambers for six weeks on two distinct serpentine soils. Accumulated metal concentrations are higher in the roots than in aerial biomass, with Ni being the most highly accumulated metal. We find total removal of Ni and Co is highest in soils of moderate metal concentrations because plants in these soils produce more biomass than ones in soils of high metal concentrations. Our data show that *B. juncea* is a potential candidate for metal phytoremediation, especially for soils with moderate levels of contamination.
Keywords: Serpentine soil, phytoremediation, *Brassica juncea*, metal extraction, nickel, cobalt, Puerto Rico.

RESUMEN

Los suelos de serpentina se caracterizan por las altas concentraciones de los metales pesados Ni, Co, Cr, Mn, Cu y Zn, los cuales son un indicador útil para el estudio de suelos contaminados por efectos antropogénicos. Con el fin de explorar el potencial de las plantas para remediar los suelos contaminados con metales, plantamos *Brassica juncea* en cámaras de crecimiento controladas durante seis semanas en dos suelos de serpentina distintos. Las concentraciones de metales acumulados son más altas en las raíces que en la biomasa aérea, siendo ni el metal más acumulado. Encontramos que la eliminación total de Ni y Co es más alta en suelos con concentraciones moderadas de metales ya que las plantas en estos suelos producen más biomasa que las de los suelos con concentraciones altas de metales. Nuestra información demuestra que *B. juncea* es un candidato potencial para la fitorremediación de metales, especialmente para los suelos con un nivel moderado de contaminación.
Palabras clave: suelo en serpentina, fitoremediación, *Brassica juncea*, extracción de metales, niquel, cobalto, Puerto Rico.

INTRODUCTION

Serpentinite is an ultra-mafic metamorphic rock enriched with many metals. Soils formed from this bedrock have high concentrations of biologically toxic elements such as Cr, Ni, Zn, Mn, Co, Cd; low concentrations of the essential plant nutrients N, P and K; low moisture-holding capabilities; and low Ca/Mg ratios (Murrent et al. 2006). This suite of properties is called the "serpentine syndrome," and it often yields either a relatively sterile landscape or highly distinct, endemic vegetation (Jenny 1980).

Plants can survive in metal-enriched soils either by actively moderating and tolerating the uptake of metals, or by suppressing their uptake (Ho et al. 2013). Plants that accumulate high concentrations of metals are known as hyperaccumulators and may be used for phytoremediation—the uptake of contaminants by plants from the soil (van der Ent et al. 2013). An ideal phytoremediator will both grow rapidly and accumulate high concentrations of a particular contaminant.

Here we study phytoremediation by using serpentine soil as a natural analog for metal-contaminated soil, and grow metal-accumulating plants in this soil. Other studies have investigated metal extraction in relation to serpentine soils; the majority of these studies analyze metal concentrations in native plants growing on serpentine soils (see Reeves et al. 1996, 1999, Chehregani 2009, Ho et al. 2013). Two past studies by students at Wesleyan University have used this method in Puerto Rico. One characterized Ni accumulation in species that grow in both serpentine and non-serpentine soil (Thomson and Fersch 2012); the other studied the potential for Cr extraction in native serpentine species (Leonard et al. 2013).

In contrast, some studies have grown plants in metal-contaminated soils in laboratory settings, and measured their capacity to extract metals (Hsiao et al. 2007, Brunetti et al. 2011, Nguyen 2011). This is the approach we adopt here, using serpentine soils as our metal-contaminated soil.

Brassica juncea

Brassica juncea is a metal accumulator that grows vigorously and tolerates a broad range of climates (Purdue University 1997). These are desirable traits for a phytoremediator. Most previous phytoremediation studies have used large, slow-growing plants; our study provides an important comparison by using an herbaceous, annual fast-growing plant.

We focus on the toxic element Ni because of its abundance in both serpentine soils and anthropogenically-contaminated soils. Nickel is an essential trace nutrient for plants, but excessive soil concentrations can cause a number of metabolic impairments, including chlorosis and stunted growth (Kirkby and Römheld 2004). High soil Ni concentrations can arise from the weathering of bed-rock containing Ni minerals, as is the case of serpentine soils; Ni contamination can also result from a number of industrial processes including the combustion of coal and other fossil fuels, mining/refining processes, and the incineration of waste (Ahmad and Ashraf 2011). Nickel is dangerous in high concentrations because of its potential to leach into groundwater systems, produce crops unsafe for human consumption, and create toxic environments in urban settings.

Research Objectives

Our study uses naturally occurring, Ni-rich serpentine soils from Puerto Rico as a proxy for anthropogenically Ni-contaminated soils. We wish to test whether *B. juncea* can survive on serpentine soils of naturally low fertility and high metal content. We aim to determine the ranges of soil metal content where *B.*

juncea can extract the greatest mass of metals, and whether it is a potential phytoremediator species.

METHODS

Field Work

Serpentine soils are found in southwestern Puerto Rico, primarily within the Maricao Commonwealth Forest (Fig. 1). There is a large serpentinite outcrop here on the north side of Route 120, west of the junction of Route 120 and Route 366 (Fig. 2). We sampled two soil types here. The first is the Nipe Clay (denoted by NcD2 in Fig. 2) along the north edge of Route 120 (18°9’5.01”N, 66°59’31.25”W). This is approximately 2.3 km west of the junction of Route 120 and Route 366. The Nipe Clay is a moderately well-drained, thick soil formed from iron-rich residuum weathered from serpentinite bedrock (USDA 2006). The second site is the Rosario Clay (denoted by RsE2 in Figure 2), which lies 2.6 km northwest of the Nipe site, also along Route 120 (18°9’38.81”N, 66°59’50.94”W). Rosario Clay is also a deep, well-drained soil formed from serpentinite bedrock (National Cooperative Soil Survey 2006).

At both sites we sampled from three soil pits 10 m apart. We collected soil by clearing all organic matter from the ground in a wide circle, digging through the roots at the top of the soil, and then collecting the soil down to a depth of 15 cm. We collected three one-gallon bags of soil from each soil pit.

Plant Cultivation

A Pakistani strain of *Brassica juncea* seeds (Accession number PI 426308) was obtained from the Agriculture Research Service of the United States Department of Agriculture. We chose this *B. juncea* cultivar because of its use in other plant extraction experiments, its ability to grow rapidly, and its wide climatic tolerance (see Zaurov 1999, Hamlin 2006, Hsiao 2007, Lai 2008).

We prepared 28 pots of soil (four replicates of each of our six soil pits plus a control potting soil) with four seeds each. We placed the pots in a controlled growth chamber (Conviron E7/2; Winnipeg, Canada) with 16 hours of light per day. We watered the pots daily, and thinned each pot to the largest two specimens. The plants grew for six weeks, at which point we separated the roots and aerial biomass from each pot. Roots were washed and shaken extensively to remove all soil. All biomass was placed in beakers and dried at 50 °C.

Soil Analysis

X-Ray Fluorescence

X-Ray Fluorescence (XRF) spectroscopy was performed on six soils (three samples of Nipe Clay and three samples of Rosario Clay) prior to plant growth. Soils were placed in an oven at 850 °C for 30 minutes to burn off organic materials and water. 7 g of soil was measured and homogenized with flux by mortar and pestle. A 1:0.3 ratio of sample to flux was maintained (Bruker Material No. K230C70, Mahlhilfe preparation pellets). Samples were pressed into pellets using a hydraulic press at 40,000 psi for four minutes and then placed in a Bruker XRF Pioneer-S4. Metal concentrations were obtained for Mn, Ni, Cr, Cu, Co, and Zn. The control soil was not analyzed by XRF; we deemed it unsafe to burn off the organic matter from the control soil because it contains perlite, which expands rapidly when heated.

Plant-Available Nutrient Cations

We combined 50 mL of 1N NH_4Cl and 2 g of unground soil in 120 mL beakers. Beakers were shaken on a shaker table for 30 minutes. Supernatant was poured into 50 mL centrifuge

Figure 1. Extent of serpentinite rock outcrops and serpentine soils in southwest Puerto Rico (Leonard et al. 2013). Geographical context of our field sites, NcD2 and RsE2, is shown.

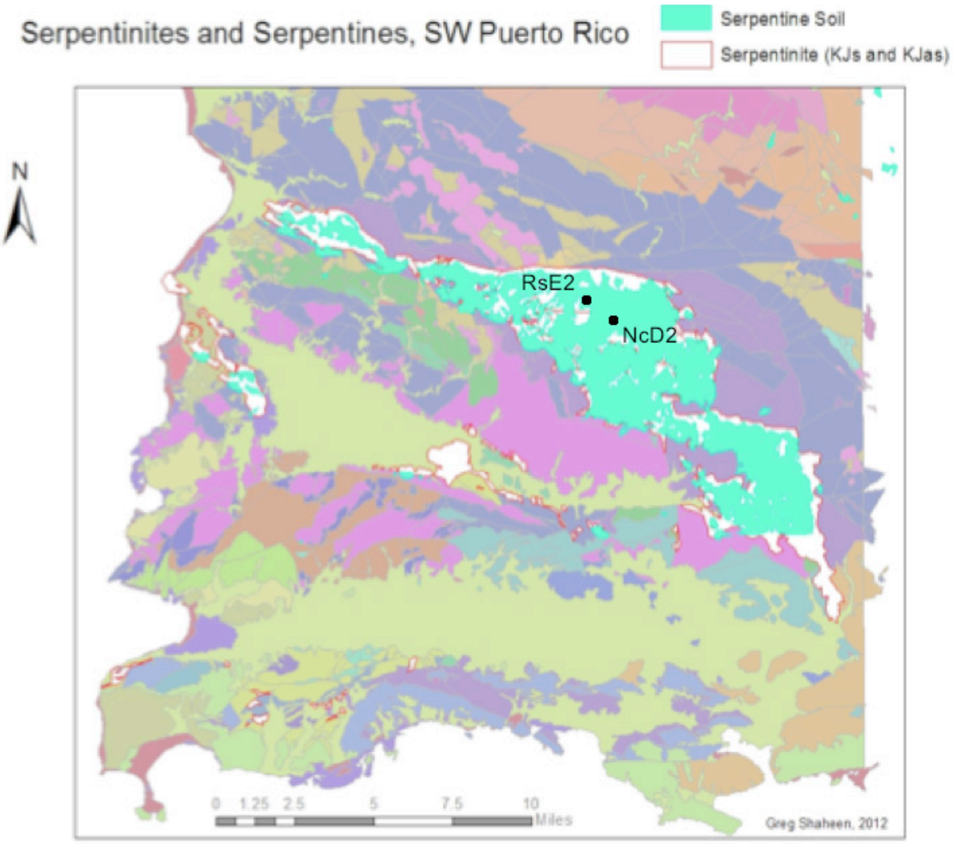
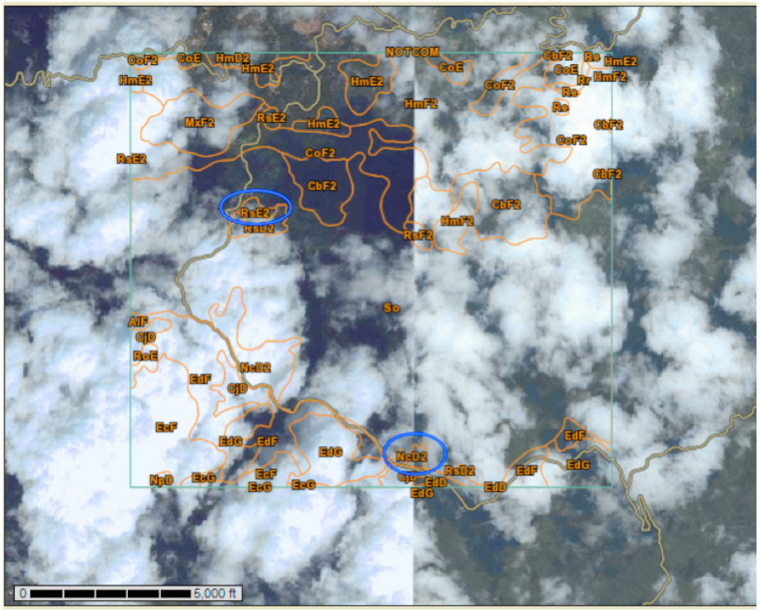


Figure 2. Map of our field sites circled, with major roads and soil types shown. So = serpentinite outcrops. NcD2 = Nipe Clay; RsE2 = Rosario Clay (USDA Web Soil Survey).



tubes and spun at 2500 rpm for 5 minutes. This extractant was removed and analyzed by ICP-OES at Amherst College for the major elements Ca, Mg, K, and Na.

Plant-Available Heavy Metals

We followed a DTPA (diethylene triamine pentaacetic acid) extraction protocol from Oze et al. (2008) to measure the concentration of plant-available metals in the soils. We prepared a solution of 0.005 M DTPA, 0.01 M $CaCl_2$, and 0.1 M triethanolamine (buffered to pH 7.3). 20 mL of this solution was mixed with 10 g of dry homogenized soil, placed in 50 mL centrifuge tubes, and then shaken for 2 hours on a shaker table. The leachate was centrifuged at 2500 rpm for 10 minutes, and then passed through a 2.5 micron sieve. We diluted 1 mL of filtered leachate with 10 mL of deionized water (DI). This solution was analyzed for trace metals using ICP-OES at Amherst College.

pH

We measured pH by mixing 5 g dry soil and 10 g DI in clean test tubes. This slurry was stirred three times over a period of 30 minutes with a glass stirrer. A standard pH probe was used to measure the pH.

Loss of Ignition

Soils were put into small ceramic bowls and then placed in an oven at 850 °C for 30 minutes to burn off organic materials. The percentage of mass lost after burning was recorded.

Plant Analysis

Trace metal concentrations of roots and shoots were determined following protocols from Oze et al. (2008). Around 2 g of plant biomass (but <1 g in the samples with low biomass production) were placed in borosilicate test tubes. Samples were ashed overnight at 425 °C. 10 mL of a 1:1 solution of trace-metal grade concentrated HNO_3 and DI was added to each test tube. Tubes were then placed in a 200 °C oven for one hour. After cooling, the tubes were centrifuged for 10 minutes at 2500 rpm. 1 mL of the extractant solution was pipetted through a 2.5 micron sieve, diluted with 10 mL DI, and placed in a refrigerator overnight.

A brown precipitate formed on the bottom of many of tubes after overnight refrigeration. This precipitate would have interfered with ICP analysis, so all tubes were centrifuged and passed through a 2.5 micron sieve again. All samples were clear afterwards and were not refrigerated again. The samples were then sent for ICP-OES analysis at Amherst College.

RESULTS

Soils

Among the six measured heavy metals, Ni and Cr register the highest concentrations (Table 1). Mean concentrations of Ni and Cr in the Nipe Clay are 14095 and 5526 ppm, respectively, and 6085 and 4099 ppm in the Rosario Clay. Total concentrations of Cr and Zn are significantly different between Nipe and Rosario soils ($p = 0.026$ and $p = 0.018$, respectively), with Nipe soils having higher concentrations of these metals.

Plant-available heavy metal concentrations in the soil are much lower than total heavy metal concentrations, and are not necessarily proportional to the total metal concentrations (Table 2). Nickel has the highest plant-available concentrations, ranging from 38 to 325 ppm, which far exceeds the concentration in the control soil (below detection limit). Three heavy metals have higher plant-available concentrations in the control soil (Cu, Cr, Zn). Only plant-available Co was significantly

Table 1. Total metal concentration of six biologically toxic elements. N = Nipe Clay; R = Rosario Clay. The control soil was not measured (see Methods). All values in ppm.

Soil	Cr	Ni	Co	Zn	Mn	Cu
R1	7546.24	4388.28	594.36	153.01	45.69	41.41
R2	3647.28	3310.64	243.36	90.95	24.01	25.25
R3	7062.64	4597.08	649.35	150.87	49.57	42.42
N1	10937.68	6045.92	428.22	309.23	37.95	37.37
N2	14190.80	3134.32	540.54	343.47	28.66	55.55
N3	17155.84	7399.64	1168.83	452.61	78.22	47.47

Table 2. Plant-available metal concentrations for all soils. N = Nipe Clay; R = Rosario Clay; C = Control potting soil. All values in ppm.

Soil	Cr	Ni	Co	Zn	Mn	Cu
R1	0.92	71.74	1.86	0.84	33.50	0.90
R2	0.56	37.74	1.70	0.46	30.64	0.06
R3	1.06	108.31	1.78	1.02	28.35	0.74
N1	4.98	278.76	3.78	5.18	84.97	0.86
N2	1.12	55.84	3.02	1.15	39.29	0.75
N3	3.04	324.62	3.41	1.17	59.21	1.30
C	46.63	0.00	0.00	47.55	96.94	6.41

different between Rosario and Nipe soils ($p = 0.015$), with Nipe soils having higher concentrations.

We find that the serpentine soils are quite low in plant-available Ca, Mg, K and Na. The average values for both Rosario and Nipe soils are far less than those of the control soil. Rosario soils are slightly higher than Nipe soils in Ca and Mg concentration, as well as the Ca/Mg ratio (Table 3), but these differences are not significant.

Nipe soils are slightly more acidic than Rosario soils (mean pH = 5.14 vs. 5.77; Table 4). This difference was significant ($p = 0.023$). The Nipe Clay also has a higher mean loss of ignition than the Rosario Clay (27.1% vs. 16.6%, respectively; Table 4), but this difference was not significant.

Plants

Biomass production varies greatly across the soils (Fig. 3). No harvestable biomass was produced at N3; the seeds germinated in N3 soil, but quickly died. Biomass production in R2 is up to an order of magnitude greater than production in the other serpentine soils. Other than soil R2, production in the serpentine soils is far less than that of the control soil.

The metal concentrations in roots and shoots show the total uptake of metals in

Table 3. Plant-available nutrient concentrations for all soils. Units are in centimoles of charge per kilogram of soil. N = Nipe Clay; R = Rosario Clay; C = Control potting soil. Concentrations in cmol/kg.

Soil	Ca	Mg	K	Na	Ca/Mg Ratio
R1	0.501	0.932	0.017	0.012	0.538
R2	0.714	0.826	0.021	0.012	0.864
R3	0.387	1.012	0.027	0.019	0.382
N1	0.499	0.992	0.114	0.027	0.503
N2	0.252	0.582	0.012	0.007	0.433
N3	0.125	0.626	0.018	0.008	0.200
C	10.951	3.688	0.488	0.308	2.969

Table 4. Soil pH and loss of ignition values. N = Nipe Clay; R = Rosario Clay; C = Control potting soil. Loss of ignition was not measured for control soil (see Methods).

Soil	pH	Loss of Ignition (%)
R1	5.84	17.56
R2	5.67	16.11
R3	5.80	15.99
N1	4.99	30.64
N2	5.04	21.07
N3	5.38	29.80
C	5.91	N/A

B. juncea over the six-week growth period (Fig. 4). Roots accumulate higher concentrations of metals than shoots. Ni accumulates at the highest concentrations, and Mn accumulates at the second-highest concentrations. This mirrors the plant available concentrations of these metals found in soils (Table 2).

Three elements (Cr, Cu, and Zn) had higher plant-available concentration in the control soil than in the serpentine soils. However, these metals were not accumulated in higher concentrations in the biomass of plants grown on control soils (see Fig. 4).

DISCUSSION

Soil Characterization

Multiple analyses were performed on six serpentine soils to determine fertility and heavy metal concentrations. The high levels of heavy metals and low soil fertility are consistent with known characteristics of serpentine soils (Oze et al. 2008). The great variability of serpentine soils in close proximity is also supported by our analyses—we find significant differences in the total Cr and Zn concentrations, plant-available Co concentration, and pH of Rosario and Nipe

Figure 3. Total biomass production in each soil as a sum of root biomass and aerial biomass (including stems and leaves). R = Rosario Clay; N = Nipe Clay; C = Control potting soil.

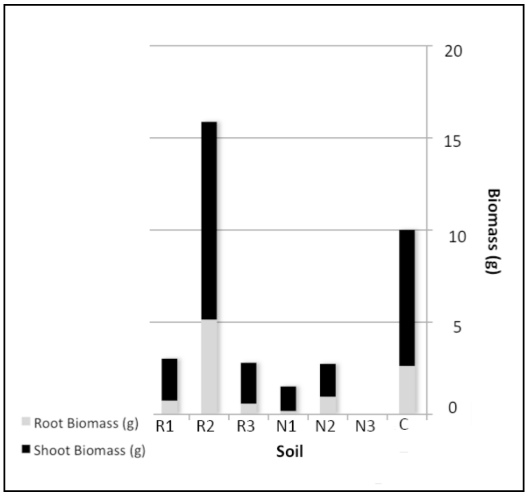
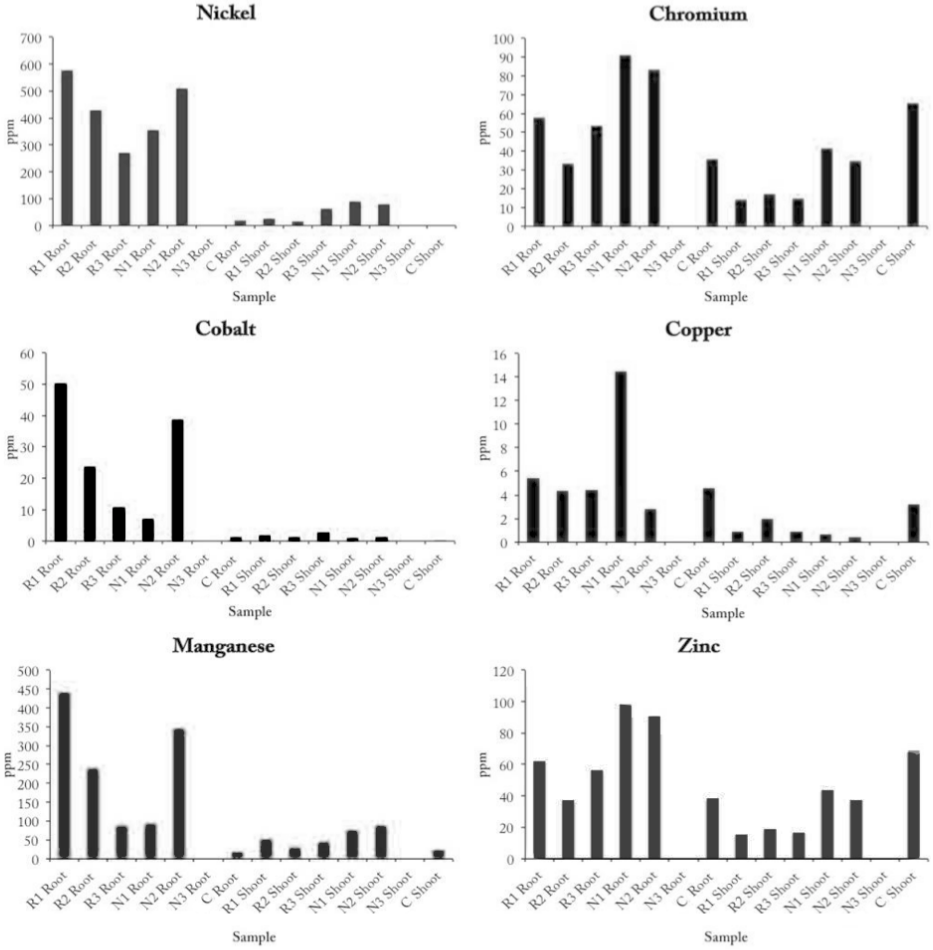


Figure 4. Concentrations of heavy metals in roots and shoots of *Brassica juncea*. The y-axis scaling differs by metal. Since there was no biomass production in soil N3, there was no biomass to analyze. N = Nipe Clay; R = Rosario Clay; C = Control potting soil.



soils. Samples within each of these soil types are also highly variable.

High metal concentrations indicate that the soils are produced from weathered serpentinite bedrock. Average total values of Ni in naturally occurring, non-serpentine soils in the United States are around 20 ppm (Ahmad and Ashraf 2011). Total Ni concentrations in the soils we sampled ranged from 3000-8000 ppm (Table 1), and plant-available Ni concentrations ranged from 37.7 to 324.6 ppm (Table 2). These plant-available concentrations are similar to published values from other sites: Oze et al. (2008) describe serpentine soils in California with available Ni ranging from 70.9 to 145.0 ppm, and Altinozlu et al. (2012) find values from 75.7 to 143.4 ppm in Turkish serpentine soils.

Poor soil fertility is ubiquitous in serpentine soils, making it difficult for plants to survive. Although many properties contribute to soil health, the plant-available Ca/Mg ratio is one widely used proxy. Values lower than 1.0 often indicate infertile soils (Schulte and Keling 1985; Stevens et al. 2005). Our soils fall below this value (Rosario mean = 0.60; Nipe mean = 0.38), while the control soil has a ratio of 2.97 (Table 3). These are also consistent with other serpentine soils: the Californian soils sampled by Oze et al. (2008) have Ca/Mg values ranging from 0.27 to 1.13.

Plant Growth Determined by Soil Properties

Since there is a wide range in biomass production across our soils, we investigate which soil traits contribute most to productivity. The plant-available Ca/Mg ratio in the soil shows a slight positive but insignificant (p = 0.580) relationship to biomass production (Fig. 5). If the control soil, an outlier, is omitted from this analysis, the relationship becomes significant (p = 0.016). This pattern is in agreement with some previous research (Hunter 1949). A similar, also insignificant (p = 0.844) relationship is found between pH and plant biomass production (Figure 6).

FIGURE 5. Plant-available Ca/Mg ratio vs. total biomass production.

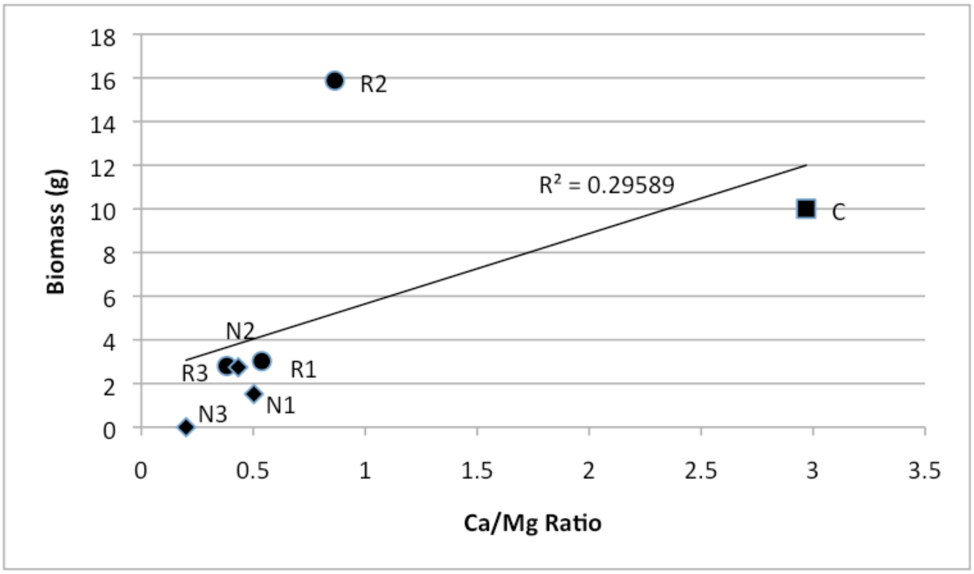
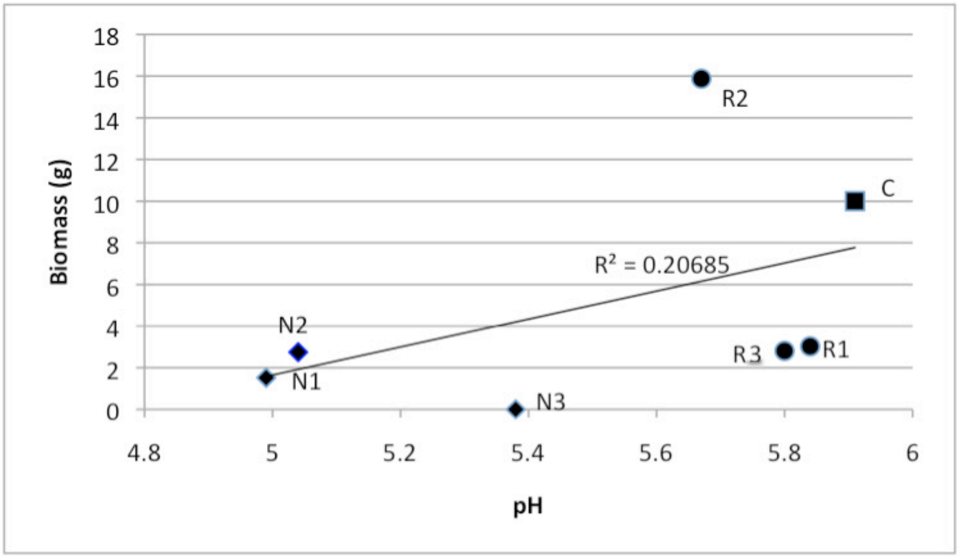


Figure 6. Soil pH vs. total biomass production.



We also compare plant-available metal concentrations and total biomass production. We observe the trend between biomass and both Ni and Co concentrations (Figs. 7 and 8). The relationships for Ni and Co are moderately strong but insignificant ($p = 0.992$ and $p = 0.493$, respectively), and show a decrease in overall biomass production at greater concentrations of available Co and Ni. Rosario 2 soil is an outlier for both of these relationships as well, with greater biomass production than expected.

We are unable to explain the extremely high biomass production from R2. Though this soil has lower metal concentrations and a higher Ca/Mg ratio than the other serpentine soils, it is unclear why it produced more biomass than even the control plants. It is possible that R2 has elevated N or P concentrations; these elements are essential to plant health, but were not measured in our study.

Phytoremediation Potential

To be an effective phytoremediator, a plant must extract a large mass of its target element. High biomass production and high metal concentration within the biomass are both needed for high metal extraction. We find that the mass of extracted metals is highest in soils of low to moderate plant-available metal concentrations (Figs. 9 and 10).

Plants grown in the control soil produce a large amount of biomass, but there is very little available Ni or Co in the soil to take up. On the other end of the spectrum, in soils with very high plant-available Ni and Co concentrations, biomass production is very low. In the N3 soil, at the high extreme of metal concentration, no biomass is produced. Even if the biomass from plants grown on soils with very high metal content had high Ni and Co concentrations, there would be little Ni or Co removal because of low biomass production. To complete this Goldilocks scenario, total metal extraction is highest at moderate levels of available Ni and Co, where growth rates are moderate to high. We have few data points to analyze, but this relationship can be seen clearly in the Ni removal amounts (Fig. 9), with plants grown on R2 soil removing the most Ni.

Figure 7. Plant-available Ni vs. total biomass production.

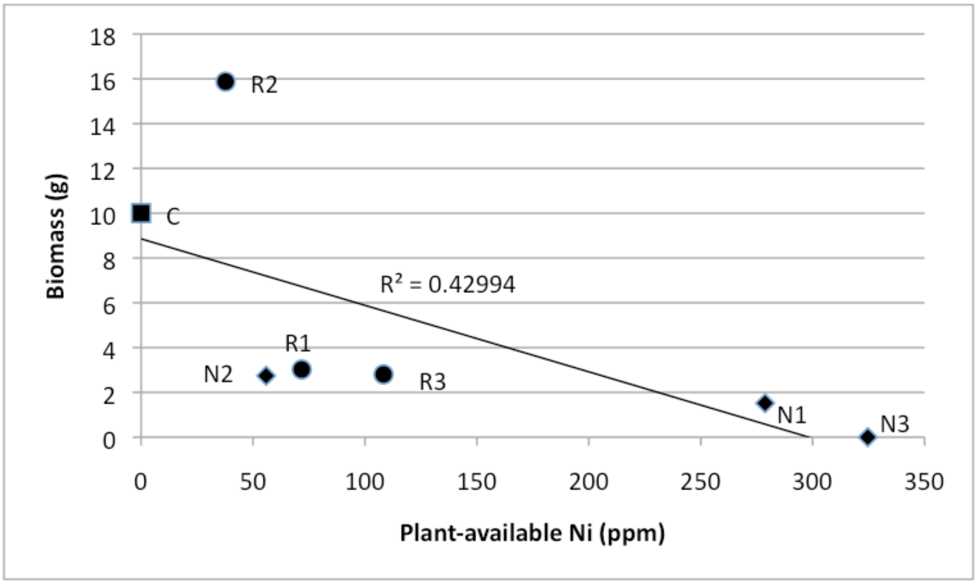


Figure 8. Plant-available Co vs. total biomass production.

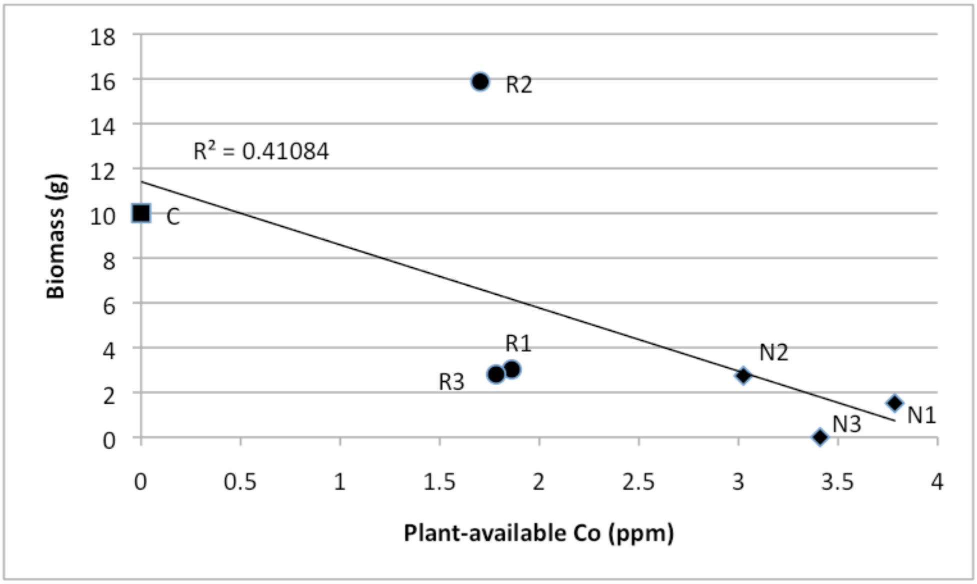


FIGURE 9. Plant-available Ni in soil vs. the total Ni removed by the plants grown on that soil.

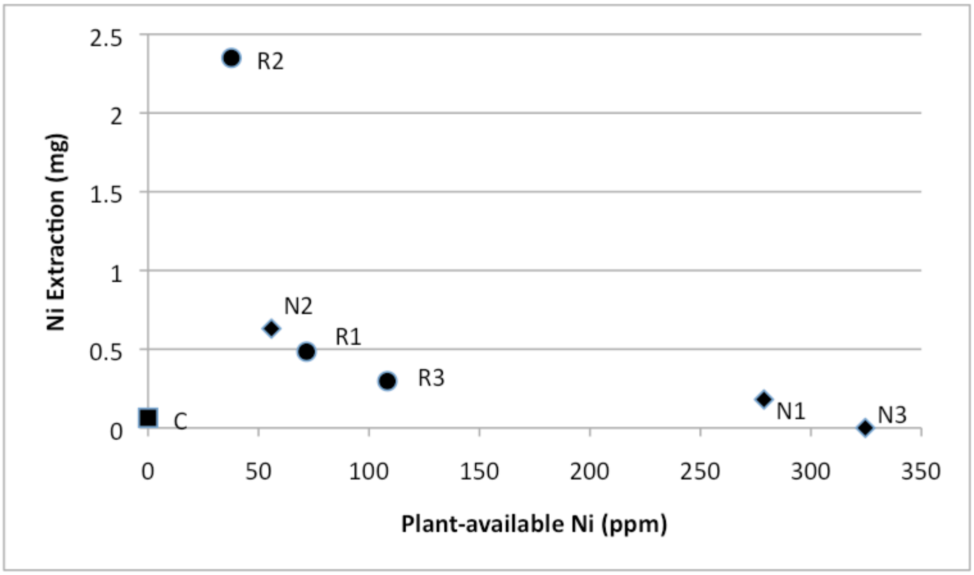
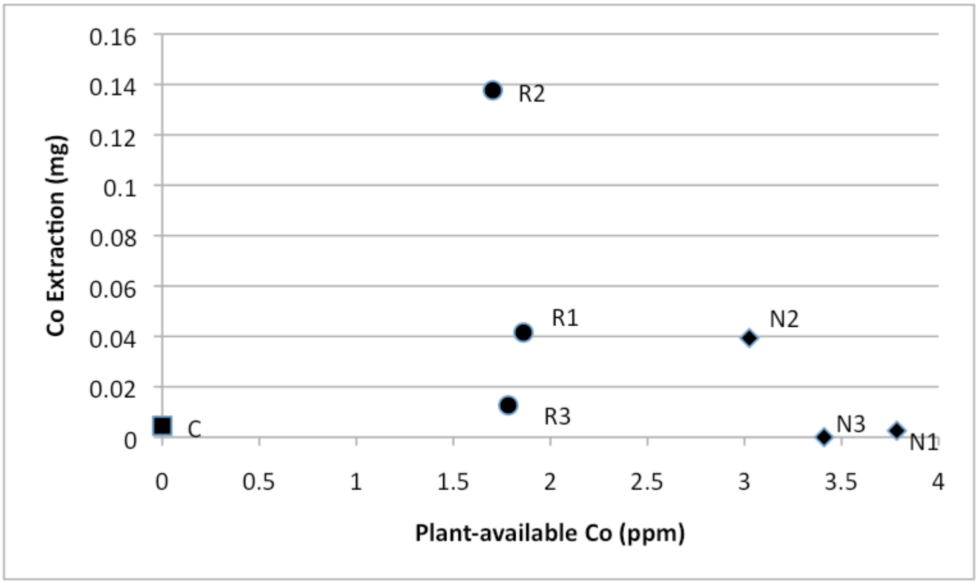


FIGURE 10. Plant-available Co in soil vs. the total Co removed by the plants grown on that soil.



Theoretical Implications

The intent of our study is to test the suitability of *B. juncea* as a metal phytoextractor on serpentine soils. We have demonstrated that *B. juncea* survives on metal-enriched soils, accumulates considerable concentrations of Ni and Co, and can in some cases produce significant biomass. These are all necessary qualities for a phytoremediator. Given its rapid biomass production, it is possible that *B. juncea* can be as effective a phytoremediator as slower-growing plants that accumulate metals at higher concentrations.

Phytoremediation is still a new and somewhat speculative field. There have been some studies investigating treatments that would increase metal phytoextraction during remediation, such as the addition of chelating agents (Hsiao 2007) or rhizobacteria (Wu 2006). Plants grown for phytoremediation would likely be fertilized to maximize biomass production and plant health, therefore increasing metal extraction. It is also likely that if *B. juncea* were used in a phytoremediation setting, it would be grown on soil that is more fertile than the serpentine soil we used in our study. If this were the case, we would expect biomass production to increase, along with total metal extraction.

A critical question is how the removal of available Ni and Co would affect soil chemistry in the long term. It is possible, for instance, that the removal of large amounts of plant-available Ni would encourage previously unavailable Ni to move into a plant-available form. If this were the case, available Ni concentrations would not drop as linearly as expected.

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EL ABANDONO AGRÍCOLA REFLEJADO EN EL CITADINO: MANEJO DE REFORESTACIÓN URBANA

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RESUMEN

El abandono agrícola resultó en la reforestación espontánea de gran parte de Puerto Rico. La mayoría de estos bosques son dominados por especies introducidas capaces de crecer en condiciones noveles creadas por el humano. Aparte de dominar terrenos agrícolas, estos bosques noveles se encuentran cada vez más en lotes abandonados en áreas urbanas. Junto a los bosques que han sido sembrados en parques urbanos, los bosques noveles urbanos son importantes para la recreación de los residentes citadinos y para servicios ecosistémicos que incluyen la protección de la biodiversidad y cuerpos de agua, la captura de carbono y la producción de madera, entre otros. En este artículo revisamos la literatura sobre los efectos de manejo sobre la estructura y composición de estos dos tipos de bosque urbano en Puerto Rico. Encontramos que el manejo en parques boscosos urbanos resulta en una menor densidad de árboles y en una mayor proporción de especies introducidas que en bosques noveles urbanos. También encontramos que, aunque ambos tipos de bosques urbanos son dominados por especies introducidas, estas especies tienden a ser ornamentales o madereras de larga vida en parques boscosos mientras que estas tienden a ser especies pioneras de corta duración en bosques noveles urbanos. La falta de manejo activo en bosques noveles urbanos permite que ocurra el proceso de sucesión natural y el establecimiento de árboles juveniles de especies nativas. Algo similar ocurre en áreas no manejadas de parques boscosos urbanos. A partir de nuestra revisión y conocimiento técnico hacemos las siguientes recomendaciones para el manejo de reforestación urbana: (1) utilizar especies nativas con valor socio-económico y resistentes a huracanes para siembras, (2) seleccionar áreas dentro de parques urbanos para permitir que el proceso de sucesión natural siga su curso, (3) proteger lotes urbanos con cobertura boscosa natural, incluyendo bosques noveles, para asegurar la conectividad del paisaje, (4) considerar la capacidad del bosque urbano para brindar servicios ecosistémicos al momento de designar protección, (5) garantizar la seguridad de transeúntes y visitantes en áreas recreativas de bosques urbanos, (6) empoderar a las comunidades para que tomen parte activa de la protección, uso y manejo de los bosques urbanos, y (7) enriquecer los bosques urbanos existentes mediante la siembra de especies nativas madereras y frutales comestibles.

Palabras clave: bosque novel, parque boscoso urbano, Puerto Rico, servicios ecosistémicos.

INTRODUCCIÓN

A mediados del siglo pasado, la sociedad citadina acostumbraba a salir de la “laja” de concreto para irse al campo los fines de semana, recrearse y darle un refresco a su mente y espíritu. Para los amantes de la naturaleza, usualmente las salidas eran a uno de dos tipos de destino: monte o playa. En el caso de los montes, los visitantes se dirigían a alguna de las reservas forestales, tal como Guajataca o El Yunque, distribuidas a través de la isla en una matriz mayormente agrícola. Todavía esto ocurre en el Puerto Rico de hoy, pero con una diferencia fundamental: la mayoría (~60%) del Puerto Rico de hoy está cubierto por bosque debido al abandono agrícola (Lugo 2014). Más aún, el abandono de lotes o terrenos cerca de o en áreas urbanas está dando paso a la reforestación espontánea de muchas áreas en la inter-fase rural-urbana e inclusive dentro de los centros urbanos de Puerto Rico (Lugo 2010, Quiñones y Abelleira 2016). El turista citadino ya no tiene que irse a una reserva para ver y disfrutar de la naturaleza que se puede encontrar en bosques naturales, incluyendo flora y fauna, y sus procesos. Puede bastar con abrir la ventana desde la oficina o dar unos pasos desde la puerta de su casa (Abelleira 2008).

En este artículo revisamos la literatura reciente sobre la estructura y composición de bosques urbanos que resultan de dos estrategias de reforestación con niveles de manejo contrastantes: siembra y sucesión natural. Específicamente, enfocamos nuestra revisión en dos tipos generales de bosque producto de reforestación: parques boscosos y bosques noveles urbanos. Con el insumo de esta revisión hacemos algunas recomendaciones prácticas para el manejo de estos bosques desde la escala local de rodal a la regional de la matriz urbana, concernientes a instituciones gubernamentales, no-gubernamentales y organizaciones comunitarias interesadas en manejar bosques urbanos para recreación, protección de biodiversidad y servicios ecosistémicos.

REFORESTACIÓN URBANA

Las áreas urbanas del Puerto Rico de hoy incluyen una vasta lista de especies de flora y fauna en ecosistemas que incluyen ríos, pastizales, humedales y bosques en diferentes estados de sucesión o edad (Abelleira 2008, Lugo 2010). Algunos de estos bosques cubren una extensión de área relativamente grande comparado a su entorno y se encuentran en áreas protegidas en la inter-fase rural-urbana, como por ejemplo el Bosque del Nuevo Milenio en Río Piedras (Lugo et al. 2005) y el Bosque Comunitario de Río Hondo en Mayagüez (Quiñones y Abelleira 2016). Estas áreas protegidas y otros bosques en áreas abandonadas en la inter-fase crean corredores que facilitan el movimiento de animales y la dispersión de semillas entre el campo y la urbe. Mientras uno se aproxima al centro urbano, las áreas boscosas tienden a volverse más pequeñas y diversas en cuanto al nivel de manejo que reciben. Algunos son áreas de arboledas sembradas en patios, parques y plazas, a los que nos referimos como parques boscosos urbanos que son manejados intensamente por brigadas de mantenimiento y ornato, y frecuentados regularmente para recreación (Lugo 2005, Román Nunci et al. 2005, Abelleira y Sanfiorenzo 2009). Otros son bosques que crecen de forma natural y espontánea en lugares abandonados como patios de casas, estacionamientos, techos de edificios y hasta áreas niveladas y pavimentadas, y pueden comprender desde hectáreas hasta decenas de metros cuadrados (Fig. 1; Chinea 2002, Lugo et al. 2011). El manejo de estos dos tipos generales de bosques urbanos, el parque boscoso urbano y el bosque *novel* urbano, varía grandemente desde poda de árboles y tala de vegetación emergente, hasta completo abandono.

¿Qué significa la novedad de estos bosques?

Al igual que los bosques emergentes en áreas agrícolas abandonadas, la mayoría de los bosques urbanos que crecen de forma natural y espontánea tienen algo en común: usualmente son dominados por especies introducidas (Lugo 2009). Esto se debe a varias razones. La principal es que el humano ha modificado las condiciones ambientales de estas áreas, sobre todo el suelo. Esto ha resultado en lotes que son dominados por especies especializadas en colonizar suelos alterados o degradados. Usualmente estas especies son gramíneas agresivas e introducidas (ej., *Panicum maximum*) que una vez colonizan el área pueden arrestar la sucesión ecológica y perpetuar el estado de pastizal (Parrotta et al. 1997, Lamb et al. 2005). En esas condiciones, especies arbóreas nativas que típicamente son las primeras en formar bosque secundario en Puerto Rico son incapaces de crecer (ej., *Cecropia schreberiana*; Silander 1979). Sin embargo y quizá inadvertidamente, el humano también ha introducido especies de árboles que están adaptados a crecer sobre estos pastizales y formar un bosque cuyo dosel típicamente termina excluyendo estas gramíneas introducidas y permitiendo el crecimiento de especies de árboles nativos (Lugo 2004). Estos bosques, denominados noveles debido a su origen antropogénico caracterizado por la dominancia de especies introducidas como resultado de la modificación de las condiciones ambientales originales, son los que mayormente encontramos creciendo de forma natural y espontánea en áreas urbanas de Puerto Rico (Lugo 2009 y 2010).

Los bosques urbanos noveles que son dominados por especies introducidas tal como *Albizia* spp. y *Spathodea campanulata* son capaces de comenzar el proceso de regeneración en condiciones ambientales noveles que incluyen suelos altamente compactados por maquinaria pesada y dominados por especies de gramíneas introducidas de crecimiento alto y denso (Chinea 2002, Lugo et al. 2005, Lugo et al. 2011, Abelleira et al. 2015, Manrique et al. 2016). Los doseles y raíces de estas especies de árboles modifican el microclima y las condiciones del suelo, facilitando el establecimiento y crecimiento de otras especies, usualmente nativas, cuyas semillas son dispersadas al lugar (Parrotta 1995, Abelleira y Lugo 2008, Abelleira 2011). Las semillas son usualmente dispersadas por animales, principalmente aves y murciélagos, que son atraídos a la copa de árboles que utilizan como perchas o que visitan para consumir frutos o néctar (McClanahan y Wolfe 1993, Abelleira 2008). Esto resulta en una mezcla de especies introducidas y nativas en gran medida favorecidas por la dieta de estos dispersores. A medida que pasa el tiempo y el bosque madura cerrando su dosel, el enriquecimiento de especies arbóreas puede aumentar en gran parte dependiendo de la proximidad del lugar a fuentes de semilla y a la disponibilidad de dispersores capaces de cruzar la matriz urbana a través de corredores boscosos o utilizando árboles aislados como peldaños para atravesar la urbe. Este efecto es mayor durante las etapas tempranas de desarrollo de la reforestación y a escalas espaciales mayores al centenar de metros entre fuente de semillas y lugar (Abelleira et al. 2015).

EFECTOS DEL MANEJO

El nivel de manejo tiene un efecto significativo sobre la estructura y composición del bosque urbano. Áreas manejadas intensivamente, tal como parques boscosos urbanos que son usados para recreación, tienden a tener una menor densidad de árboles y una mayor representación de especies introducidas que bosques noveles urbanos que no son manejados (Tabla 1). El manejo en estos parques boscosos urbanos generalmente consiste en la eliminación de crecimiento de vegetación en el sotobosque, incluyendo árboles juveniles, herbáceas o malezas, por maquinaria (ej., *trimmers* y podadoras)

Figura 1. Cualquier rincón abandonado de las áreas urbanas puede servir como foco de regeneración boscosa. En este caso, un árbol de tulipán africano (*Spathodea campanulata*) se encuentra creciendo y floreciendo en una hendija en el pavimento dentro de un pequeño lote abandonado en el casco urbano de Río Piedras.

de brigadas de mantenimiento y ornato municipal. Esto previene el crecimiento de árboles adicionales a los allí plantados por el humano, redundando en menor densidad de árboles. A su vez, los árboles plantados en parques boscosos tienden a ser de especies introducidas lo cual se refleja en la prevalencia de estas especies en áreas manejadas (Tabla 1). En contraste, muchas o la mayoría de las especies de árboles que crecen como juveniles en bosques noveles urbanos son nativas debido en gran parte a la dispersión de semillas de estas especies por fauna, dada la posibilidad de crecimiento en la ausencia de mantenimiento (Abelleira y Sanfiorenzo 2009, Abelleira et al. 2015). Esto hace que los bosques noveles urbanos tengan posiblemente un valor mayor para la protección de la biodiversidad nativa que los parques boscosos que son manejados activamente por brigadas de mantenimiento y ornato.

Los casos de bosques riparios urbanos documentados en Puerto Rico proveen apoyo adicional a la prevalencia de los patrones de efectos de manejo descritos (Tabla 1). Una porción significativa, o la mayoría, del bosque ripario del Río Piedras está sujeto a mantenimiento similar al de parques boscosos (Lugo et al. 2001). En contraste, el bosque ripario de la Quebrada Chiclana, que fue producto de un proyecto de mitigación ambiental, no ha sido sujeto a ningún tipo de manejo desde la restauración inicial (Manrique et al. 2016). El bosque ripario manejado contiene una densidad de árboles menor y una mayor representación de especies introducidas que el bosque no manejado. Curiosamente, ambos de estos bosques riparios están dominados por la misma especie introducida y fijadora de nitrógeno, *Albizia procera* (Tabla 1).

La dominancia de especies introducidas en bosques urbanos es general, independientemente del nivel de manejo; todas las especies dominantes en los estudios revisados son introducidas (Tabla 1). Sin embargo, las especies introducidas dominantes en parques boscosos urbanos son plantadas por el humano y típicamente no constituyen parte de la sucesión natural en bosques noveles. Este es el caso de la caoba (*Swietenia* spp.) y del padauk de Burma (*Pterocarpus macrocarpus*), los cuales son plantados por la calidad de su madera y la vistosidad de sus flores, respectivamente (Lugo 2005). Estas especies son de larga duración y tienden a ser más resistentes a huracanes (Francis 2000, Duryea et al. 2007). En contraste, las especies introducidas dominantes en bosques noveles tienden a tener rasgos correspondientes a especies pioneras, como dispersión por viento, rápido crecimiento e intolerancia a sombra, lo cual las hace capaces de colonizar áreas deforestadas y abandonadas sin la ayuda del humano. Sin embargo, la pobre calidad de la madera asociada a estos rasgos las hace más susceptibles a huracanes y patógenos (Francis 2000, Duryea et al. 2007, Abelleira et al. 2015). Ejemplos notables de estas especies son *A. procera*, *Leucaena leucocephala* y *S. campanulata*, la última siendo la especie más abundante en Puerto Rico (Marcano et al. 2015). En el caso del bosque experimental de la Universidad de Puerto Rico (UPR), *L. leucocephala* fue plantada cerca del lugar lo cual facilitó su colonización y dominancia en este sitio del norte húmedo de Puerto Rico (Tabla 1; Abelleira et al. 2015). La especie *L. leucocephala* es más común y dominante en áreas secas del sur (Marcano et al. 2015).

Los patrones de riqueza de especies bajo diferentes niveles de manejo son poco claros. Esto puede ser en parte debido a las diferentes áreas de muestreo usadas por los estudios revisados (Tabla 1). Otras razones con consecuencias más prácticas son los mecanismos que influencian la riqueza de especies encontradas en parques boscosos *versus* en bosques noveles urbanos. En los parques boscosos manejados, la mayoría de las especies de árboles son

Tabla 1. Densidad de árboles y juveniles, y riqueza, origen y dominancia de especies de árboles y juveniles en parques boscosos, bosques noveles y bosques riparios en áreas urbanas de Puerto Rico. Celdas en blanco denotan ausencia de datos.

Sitio	Densidad de Árboles (árboles/ha)	Densidad de Juveniles (juveniles/ m^2)	Riqueza de Especies de Árboles (área muestreada en ha)	Riqueza de Especies de Juveniles (área muestreada en m^2)	Especies Introducidas de Árboles (%)	Especies Introducidas de Juveniles (%)	Especie Dominante de Árboles (Dominancia Relativa en %)	Especie Dominante de Juveniles (Dominancia Relativa en %)	Fuente
Parque Boscoso Urbano									
Parque el Paraíso, Río Piedras*	127		37 (1.1)		76		*Swietenia macrophylla x mahogany* (24)		Román et al. 2005
Parque V Centenario UPR, Río Piedras^	96	10	35 (1.2)	12 (60)	71	58	*Pterocarpus macrocarpus* (36)	*Pterocarpus macrocarpus* (51)	Abelleira & Sanfiorenzo 2009
Bosque Novel Urbano									
Bosque del Nuevo Milenio, Río Piedras*	1562		53 (1.0)		26		*Spathodea campanulata* (27)		Lugo et al. 2005
Bosque Experimental UPR, Toa Baja[#]	1241	19	18 (0.4)	22 (90)	38	24	*Leucaena leucocephala* (56)	*Leucaena leucocephala* (45)	Abelleira et al. 2015
Bosque Ripario Urbano									
Río Piedras[+]	300		14 (0.4)		86		*Albizia procera* (30)		Lugo et al. 2001
Quebrada Chiclana, San Juan[+]	2800		35 (0.4)		34		*Albizia procera* (46)		Manrique et al. 2016

Notas: * árboles ≥4cm de diámetro a altura de pecho (DAP); ^ árboles ≥3cm DAP y juveniles <3cm DAP; [#] árboles ≥5cm DAP y juveniles <5cm DAP; y [+] árboles ≥2.5cm DAP.

plantadas. Usualmente, estas siembras se hacen para incluir una gran variedad de especies madereras u ornamentales que en su mayoría son introducidas. En contraste, la riqueza de especies en el bosque novel urbano depende en gran medida del proceso natural de dispersión que, en Puerto Rico, favorece especies nativas dispersadas por animales voladores como aves y murciélagos (Rodríguez Durán 2005, Abelleira 2010, Lugo et al. 2012, Abelleira et al. 2015). Cuando un área de parque boscoso urbano es dejada a merced del proceso de sucesión natural de dispersión y crecimiento, se puede observar el influjo y establecimiento de especies nativas dispersadas por animales. Por ejemplo, en áreas no manejadas del Parque V Centenario en la UPR de Río Piedras se puede observar una alta densidad de árboles juveniles que asemeja la encontrada en un bosque novel urbano en Toa Baja (Tabla 1; Abelleira y Sanfiorenzo 2009, Abelleira et al. 2015). Aunque la proporción de especies introducidas de juveniles es más alta en este parque boscoso que en el bosque novel, especies nativas que no están presentes como árboles parentales en el parque están llegando al lugar por dispersión natural mediada por animales, y están creciendo y enriqueciendo estas áreas del parque urbano (Abelleira y Sanfiorenzo 2009). Al igual que los bosques noveles, los parques boscosos urbanos están siendo visitados por dispersores de semillas lo cual significa que también sirven de corredores que facilitan el movimiento de estos animales a través de la matriz urbana.

RECOMENDACIONES DE MANEJO

Las siguientes recomendaciones de manejo para bosques urbanos, particularmente para parques boscosos y bosques noveles urbanos producto de la reforestación por siembra y sucesión natural, emergen de esta revisión de literatura, y del conocimiento académico y técnico de los autores:

1. En tiempos más recientes, el enfoque de la siembra de árboles en áreas urbanas ha cambiado del uso mayoritario de especies introducidas a uno que cada vez más incorpora el uso de especies nativas en el diseño paisajista de parques y áreas verdes (González 2002). Esto debe seguir así para proteger la biodiversidad nativa. En particular, especies madereras nativas a Puerto Rico o la región del Caribe pueden tener no solo un mayor valor para la producción de materia prima, sino que también pueden ser más resistentes a disturbios naturales tal como huracanes (Francis 2000, Lugo 2005, Duryea et al. 2007).

2. Seleccionar áreas dentro de parques urbanos para dejar que el proceso de sucesión natural siga su curso de forma similar al que ocurre en bosques noveles es deseable para incrementar la capacidad de proteger la biodiversidad y el valor recreacional. Hay que reconocer que, debido a la modificación humana, muchas áreas solo van a poder ser colonizadas naturalmente por especies introducidas adaptadas a crecer en dichas condiciones. Permitir que dicho proceso de sucesión natural proceda tendrá el efecto de enriquecer la diversidad de especies de flora y fauna en el lugar. También puede ser atractivo para visitantes interesados en el senderismo natural y la observación de la vida silvestre, potencialmente incrementando el ecoturismo en áreas de bosques urbanos.

3. Áreas urbanas abandonadas donde se esté dando un proceso de sucesión natural hacia el establecimiento de bosque, incluyendo bosques noveles, deben ser consideradas para ser protegidas a corto o largo plazo con el propósito de aumentar y preservar la

conectividad del paisaje urbano para el movimiento de animales y la dispersión de semillas. Esto es más relevante cuando se trata de lotes que han estado en abandono por un tiempo significativo, permitiendo el cierre del dosel y la madurez estructural en el proceso de sucesión ecológica de un bosque. El cierre del dosel incrementa las visitas por fauna adaptadas a condiciones de bosque, y modifica el microclima del sotobosque favorablemente para el establecimiento y crecimiento de especies arbóreas.

4. La capacidad de bosques urbanos para brindar servicios ecosistémicos específicos debe ser considerada al momento de evaluar la posibilidad de proteger áreas de bosques urbanos. Por ejemplo, la localización de bosques en ciertas áreas, como contiguos a humedales o zonas riparias, los pueden hacer más útiles para servicios de protección de calidad y cantidad de agua (Lugo 2010, Lugo et al. 2011, Brandeis et al. 2014). Similarmente, la localización de bosques en ciertas áreas puede aumentar el valor escénico de la vecindad y promover la actividad turística, y reducir gastos energéticos asociados al enfriamiento de casas y edificios, aumentando la capacidad de la reforestación para reducir la huella de carbono urbana (Lugo et al. 2011, Brandeis et al. 2014). Todo esto puede redundar en beneficios económicos para comercios adyacentes. En adición, los bosques urbanos pueden ser fuente de maderas valiosas como la caoba (*Swietenia* spp.) que muchas veces son desperdiciadas luego de podas y cortes para mantenimiento (Lugo 2005). Instituciones gubernamentales y la empresa privada podrían desarrollar programas para asegurar el aprovechamiento de estos servicios ecosistémicos.

5. La seguridad tiene que ser garantizada en áreas de bosques y vegetación urbana si van a ser usadas para recreación. Los ejemplos de áreas verdes urbanas en barbecho que sirven de manto para actividades criminales abundan (ej., El Nuevo Día 2014, Celona y Marino 2016). Nuestra propia experiencia en trabajos de campo o durante recreación en bosques urbanos o en la inter-fase rural-urbana sugiere que se necesita un manejo para el control de vegetación emergente o malezas, y vigilancia periódica en áreas contiguas a veredas de bosques urbanos que van a ser usados intensivamente para recreación. El establecimiento, mantenimiento e identificación de veredas para este propósito, así como vigilancia preventiva, son algunas actividades que pueden garantizar la seguridad.

6. Ejemplos existentes de bosques noveles urbanos que son manejados para múltiples usos demuestran la importancia del empoderamiento comunitario para la protección de estas áreas y para establecer un manejo apropiado. Un ejemplo ideal es el Bosque Comunitario de Río Hondo en Mayagüez (Fig. 2; Quiñones y Abelleira 2016). La comunidad aledaña a este bosque se organizó cuando se dio a conocer que en el área iba a ser desarrollado un proyecto residencial. Esta auto-organización resultó en una propuesta que ganó fondos municipales y federales para la compra del predio y su protección a perpetuidad. Otros ejemplos emergentes lo son el Bosque Comunitario del Barrio Puntas en Rincón y el Bosque

Comunitario de Punta Borinquen en Aguadilla. La participación comunitaria es el componente crucial para el éxito de la silvicultura y foresteria urbana de base comunitaria (Lugo 2012). En la medida que el desparrame urbano aumente, estas organizaciones comunitarias jugarán un papel más importante en la protección de bosques urbanos. La coalición entre organizaciones puede aumentar la capacidad de conservar estos bosques.

7. El manejo silvicultural en bosques noveles urbanos puede incluir el enriquecimiento de rodal mediante la siembra de especies ausentes. Esto puede incluir tanto especies nativas madereras como especies frutales para consumo humano. El establecimiento de bosques noveles puede modificar el microclima y suelo del sitio favorablemente, creando una oportunidad para el establecimiento y crecimiento exitoso de árboles juveniles sembrados en el sotobosque (Abelleira 2011, Abelleira 2016). En adición a especies nativas madereras u ornamentales, la siembra de árboles en parques urbanos también podría incluir especies frutales. El enriquecimiento de bosques noveles y parques boscosos urbanos con especies frutales eventualmente puede proveer insumos alimenticios y económicos a comunidades aledañas, y contribuir al desarrollo de seguridad alimentaria.

CONCLUSIÓN

Nuestra revisión se enfocó en dos tipos generales de bosques urbanos producto de la reforestación los cuales consideramos muy relevantes debido a su creciente expansión y uso por los residentes citadinos. Las clasificaciones de bosques urbanos en Puerto Rico reconocen otros tipos de bosques urbanos tal como corredores artificiales, los cuales consisten mayormente en hileras de árboles sembrados a orillas de carreteras, y bosques primarios o secundarios que ocurren como remanentes de la cobertura de vegetación original dentro de la matriz urbana, principalmente manglares en humedales y bosques en mogotes (Lugo 2002, Suárez et al. 2005, Lugo et al. 2011, Brandeis et al. 2014). Bajo nuestra revisión, los efectos y recomendaciones de manejo correspondientes a los parques boscosos urbanos aplican similarmente a los corredores artificiales. Los remanentes de bosque primario o secundario albergan comunidades de especies mayormente nativas y hasta poblaciones de especies en peligro de extinción, como es el caso del palo de rosa (*Ottoschultzia rhodoxylon*) en mogotes del Bosque Santa Ana en el Parque Monagas en Bayamón (Suárez et al. 2005; Ilianet Morales, comunicación personal). En la medida que sea posible, estos lugares deben ser preserva-dos en su totalidad y su manejo se debe minimizar al mantenimiento de veredas para senderismo. Sin embargo, se debe reconocer que la novedad de los bosques urbanos, tanto parques boscosos como bosques noveles, aumenta no solo el potencial local de estos lugares para la protección y restauración de la biodiversidad, sino que también contribuyen a lograr los mismos propósitos a una escala regional mediante la facilitación de la dispersión de flora y fauna entre remanentes de bosque nativo y lugares donde se permite la sucesión natural. Los parques boscosos y bosques noveles urbanos también pueden apoyar otros servicios ecosistémicos como la protección de cuerpos de agua, captura de carbono y la belleza escénica. No se debe menospreciar el valor biológico, ecológico y

Figura 2. Vista aérea del Bosque Comunitario de Río Hondo en la inter-fase rural-urbana de Mayagüez. Nótese la posición estratégica de este bosque como parte de un cinturón boscoso que sirve de conector entre la vegetación de la costa y la montaña.

socio-económico de estos bosques. Nuestras instituciones deben promover la protección de los bosques urbanos que le dan vida a la urbe y la hacen más placentera para el residente citadino, mejorando su calidad de vida.

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STRUCTURE, GROWTH RATES, AND CARBON SEQUESTRATION OF AN URBAN FOREST IN RÍO PIEDRAS, PUERTO RICO

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ABSTRACT

We studied the Dr. Julio Víctor Rivera urban forest in Río Piedras, Puerto Rico and found 42 tree species (12 native and 30 introduced), with an addition of 5 species since 2007. The most common species was hybrid mahogany *(Swietenia macrophylla x mahogony*). We found 6 trees that had established naturally, implying that the forest is capable of regenerating and diversifying. The mean diameter at breast height and tree height were 31.5 cm (±1.5, n = 233) and 14.5 m (±0.43, n = 233), respectively. The total basal area of the forest was 25.3 m²/ha. Growth rates varied over 14 years. The above ground biomass was 232 Mg/ha with an increase of 17.8 Mg/ha·yr. Carbon sequestration was equivalent to 9 Mg C/ha·yr. Volume estimation based on the assessment of all branches was 19 percent less than the volume obtained from the product of basal area and height. The species composition of this forest reflects the preferences of the residents of El Paraíso that manage the forest.This forest with measurable ecological value can serve as a model for other urban areas.

Keywords: Novel forests, aboveground carbon, tree volume, hybrid mahogany, forest biomass.

RESUMEN

Estudiamos el bosque urbano Dr. Julio Víctor Rivera en Río Piedras, Puerto Rico y encontramos 42 especies arbóreas (12 nativas y 30 introducidas), con un aumento en 5 especies desde 2007. La especie más común es la caoba híbrida (*Swietenia macrophylla x mahogany*). Encontramos 6 árboles que se establecieron naturalmente, implicando que el bosque tiene potencial de regeneración y diversificación. El diámetro a altura de pecho y altura promedio fueron 31.5 cm (±1.5, n = 233) y 14.5 m (±0.43, n = 233), respectivamente. El área basal total del bosque fue de 25.3 m²/ha. Las tasas de crecimiento variaron a través de 14 años. Estimamos una biomasa aérea de 232 Mg/ha con un crecimiento de 17.8 Mg/ha·año. Se calculó también el secuestro de carbono, que fue equivalente a 9 Mg C/ha·año. El estimado de volumen por árbol basado en la medición de todas las ramas y tronco fue 19 por ciento menos que el volumen obtenido a través del producto de área basal y altura. La composición de especies de este bosque urbano refleja las preferencias de los residentes de El Paraíso que lo manejan. Este bosque es de valor ecológico medible que podría servir de modelo para otras áreas urbanas.

Palabras clave: Bosques noveles, almacenaje de carbono, volumen de madera, caoba híbrida, biomasa del bosque.

INTRODUCTION

Urban areas in Puerto Rico cover up to 11 percent of the country's land area (Martinuzzi et al. 2007) and 6 percent of Puerto Rico's forest cover is found in these urban areas (Martinuzzi et al. 2013). These green areas in urban zones are considered urban forests and have different origins. Depending on the level of management, their species composition, growth, and structure can vary greatly (Román et al. 2005). Besides having high recreational and aesthetic value, urban forests provide multiple services to adjacent communities. They can reduce the heat island effect and – consequently- reduce energy consumption in homes and buildings due to cooling or air conditioning. This is especially important, since studies have found that San Juan has experienced an increase in temperature of 0.06 °C/yr for more than 40 years due to the heat island effect (Velázquez Lozada et al. 2006). Also, reforestation in tropical areas can offset atmospheric carbon concentrations at different rates depending on past land use (Silver et al. 2000). Trees in urban forests also remove atmospheric carbon (Nowak and Crane 2002). In this study, we seek to understand the change in species composition, structure, and growth of an urban forest that has been studied on three separate occasions through approximately 14 years. Additionally, on this occasion we estimated the aboveground biomass and carbon sequestration of the forest.

STUDY SITE

The Dr. Julio Víctor Rivera urban forest in Río Piedras, Puerto Rico (18°22'54.5"N 66°03'43.0"W) was established by residents of the surrounding community in 1988. Its composition is representative of the preference of residents and the availability of seeds and seedlings from local nurseries (Román et al. 2005). The forest has an area of 1.0785 ha. It is a space highly visited by residents for recreational motives and with that, it has multiple interventions given their preferences; it has hardly any understory, for example (Román et al. 2005). This forest was first studied in 2001 and has been studied three times ever since, including this occasion.

METHODS

We first began this study in early February, 2015 by identifying all the listed trees from the most recent inventory (2007). We tagged those trees that were still alive and took note of those that had died. Tree height was determined using a LaserAce® Hypsometer. The Diameter at Breast Height (DBH) was taken at 1.37m height with a tape adjusted to measure diameter. Finally, we identified those new trees in the study site (ingrowth), identified them to species, and measured their height and DBH. Tree basal area was determined using the following formula:

$$\text{Basal Area} = \pi(\text{DBH}/2)^2$$

The total basal area of the forest was the sum of the basal area of every stem measured at DBH, including each stem of trees with multiple stems. We calculated diameter, height, and basal area growth rates, subtracting from the result the value of the last measurements taken. This was divided by the amount of time between both dates and expressed in growth per year. We calculated the average diameter, height, and basal area for each tree species and determined their relative density dividing the number of stems per species by the total number of stems in the forest. Relative basal area of each species was determined by dividing the total basal area of each species by the total basal area of the forest. We calculated the Importance Value by adding the species' relative density and relative basal area and dividing the result by two. This was done for every species. In addition, we calculated the density of stems, the density of trees, and tree basal area per hectare per species dividing each of these parameters by the forest area. Mortality rate was expressed as percent/year·ha. All calculations were performed using Microsoft Excel.

The measure of tree diameter and height is pretty trustworthy to determine tree volume in a precise manner (Condit 2008). However, in urban conditions, trees tend to branch excessively precluding an accurate estimate of volume from a single DBH and height measurement. Therefore, we chose four trees among those with the highest volume within the forest to measure their volume branch by branch, to compare the difference – if any- in volume as a result of both methods used.

Each of the chosen trees was sketched with the highest detail for the purpose of comparing their structure (Fig. 1). We measured the length and the diameter of each branch until the divergence point into two other branches, in which case we proceeded to measure each individual divergence until the point where the branches were unmeasurable or smaller than 4 cm in diameter. To measure length of the ranches we used a LaserAce® Hypsometer and for diameter we used a pentaprism or a measuring tape calibrated for diameter. The tree volume was the sum of all the individual volumes of the branches and main stem using the equation described above for basal area multiplied by the length of the branch. The difference in volume of each tree between this new method and the method using basal area and height was computed as a percentage. The resulting values of the 4 trees studied were averaged. The result was applied as a correction factor (0.8132) to the volume of the rest of the trees in the forest.

The sum of all tree volumes was divided by the forest area to express volume on a hectares basis. We followed Brown (1997) for calculating tree aboveground biomass. We multiplied the volume of each tree by its species wood density. Wood densities of species were found using different literature sources (e.g., Reyes et al. 1992). For those tree species for which we did not find wood density information, we applied the average wood density for trees in moist tropical America: 0.60 g/cm³ (Reyes et al. 1992). The weighted average wood density of the forest was calculated by dividing the sum of the biomass of all trees by the total volume of the forest. We determined total aboveground biomass (or biomass density) by multiplying the total forest volume per hectare by the average wood density, all divided by 10^6 to express the estimate in Megagrams. To estimate biomass increase rate, we subtracted the aboveground biomass from 2007 to the biomass from 2015 and divided the result by the time passed in years. Assuming that half of the total biomass is made of carbon, we determined carbon sequestration as half the increase in biomass.

RESULTS

Species Composition and Importance Value

The forest increased in species richness, with 5 new species not found before in 2007 (Fig. 2). However, there were a few corrections made regarding species identification in 2007. *Ficus lutea*, for example, was considered *Ficus benjamina* in 2007. On the other hand, one tree was wrongly considered dead in 2007 (*Psidium guajava*), and was therefore not considered as part of the species composition during that time. The new species found as new individuals were *Annona reticulata,*

Figure 1. Example of a tree used for the new method of volume estimation. All branches were sketched for the purpose of comparing volume results with estimates based on diameter and height.

Figure 2. Species Importance Value Curve demonstrating species dominance over two different periods and showing species increase in 2015.

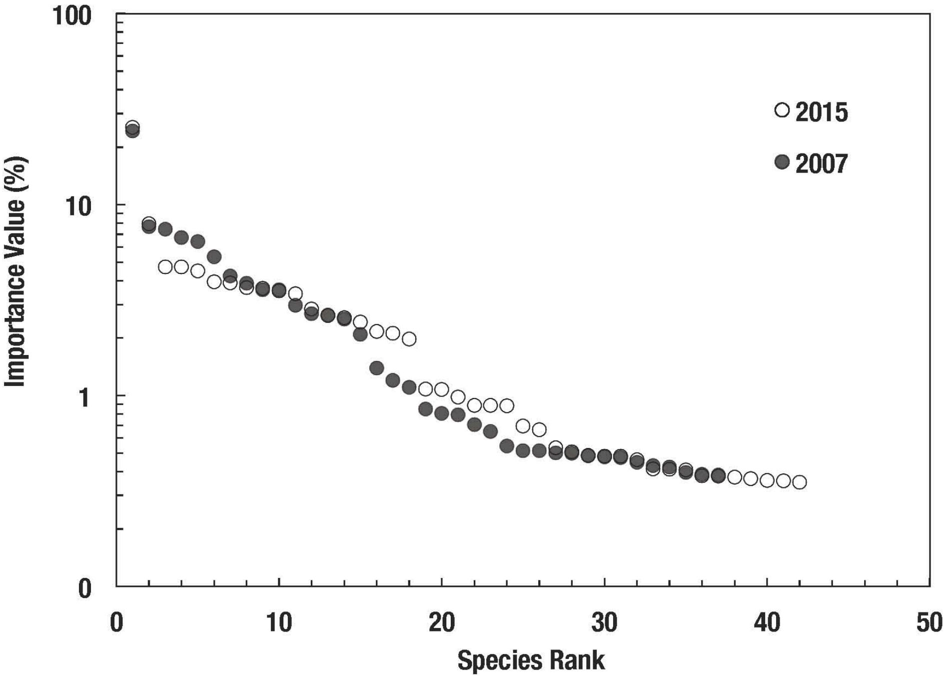


Table 1. Tree species in the Dr. Julio Víctor Rivera urban Forest of the El Paraíso Urbanization. Species are in order of percent Importance Value (IV). Also, average diameter at breast height (DBH) and tree height (along with their standard error of the mean), basal area and stem and tree density per species.

Species	Stems	Average DBH (cm)	Average Height (m)	Density (stems/ha)	Density (trees/ha)	Basal Area (m²/ha)	IV
Swietenia macrophylla x mahagoni	31	54.7 (26)	18.8 (5.2)	28.7	25.0	8.2	25.4
Pterocarpus indicus	20	40.9 (23)	26.1 (3.4)	18.5	4.6	3.2	7.9
Tabebuia heterophylla	20	22.5 (8.7)	14.2 (2.3)	18.5	8.3	0.8	4.7
Lagerstroemia speciosa	20	28.6 (11)	11.8 (3.7)	18.5	5.6	1.4	4.7
Ficus benjamina	1	170.0	28.3	0.9	0.9	2.1	4.5
Terrminalia catappa	9	25.2 (6.9)	10.9 (4.5)	8.3	8.3	0.4	3.9
Cordia sebestens	12	16.5 (3.4)	5.8 (1.3)	11.1	9.3	0.3	3.9
Areca catechu	10	14.0 (1.6)	7.6 (2.1)	9.3	9.3	0.1	3.7
Callistemon citrinus	15	19.1 (8.4)	9.9 (2.2)	13.9	7.4	0.5	3.6
Tabebuia rosea	6	39.0 (16)	20.9 (3.8)	5.6	5.6	0.8	3.5
Swietenia mahagoni	6	44.1 (7.2)	20.7 (4.0)	5.6	4.6	0.9	3.4
Melaleuca quinquenervia	9	27.1 (13)	13.8 (3.1)	8.3	4.6	0.6	2.8
Swietenia macrophylla	5	38.8 (18)	18.5 (3.5)	4.6	3.7	0.6	2.6
Peltophorum pterocarpum	4	43.9 (42)	14.6 (8.1)	3.7	1.9	1.0	2.6
Roystonea borinquena	4	42.2 (9.7)	17.4 (0.68)	3.7	3.7	0.5	2.4
Eucalyptus robusta	4	43.1 (13)	23.1 (6.8)	3.7	2.8	0.6	2.2
Delonix regia	6	40.2 (8.4)	13.3 (0.41)	5.6	1.9	0.7	2.1
Ficus lutea	2	71.7 (33)	17.6	1.9	0.9	0.8	2.0
Cassia fistula	6	20.4 (7.8)	15.0 (4.2)	5.6	1.9	0.2	1.1
Ceiba pentandra	1	71.5	23.8	0.9	0.9	0.4	1.1
Montezuma speciosissima	5	20.1 (4.3)	14.9 (1.8)	4.6	1.9	0.2	1.0

Table 1. (continued)

Species	Stems	Average DBH (cm)	Average Height (m)	Density (stems/ha)	(trees/ha)	Basal Area (m²/ha)	IV
Tabebuia glomerata	7	14.1 (3.2)	10.3 (1.6)	6.5	1.9	0.1	0.9
Cecropia sceveriana	2	26.0 (11)	16.9 (4.0)	1.9	1.9	0.1	0.9
Cassia javanica	4	18.6 (7.8)	12.5 (4.2)	3.7	1.9	0.1	0.9
Calophyllum calaba	2	6.0 (2.1)	6.6 (0.57)	1.9	1.9	0.0	0.7
Tamarindus indica	4	22.6 (8.5)	12.0 (2.3)	3.7	0.9	0.2	0.7
Mangifera indica	1	36.7	10.5	0.9	0.9	0.1	0.5
Chrysophyllum cainito	4	16.0 (7.1)	9.0 (4.1)	3.7	0.9	0.1	0.5
Syzigium malaccense	1	31.8	15.6	0.9	0.9	0.1	0.5
Melicoccus bijugatus	1	31.5	12.0	0.9	0.9	0.1	0.5
Tabebuia aurea	1	31.3	13.5	0.9	0.9	0.1	0.5
Cananga odorata	1	29.1	9.2	0.9	0.9	0.1	0.5
Petitia domingensis	1	22.7	13.9	0.9	0.9	0.0	0.4
Pimenta racemosa	3	12.3 (4.9)	12.7 (0.00)	2.8	0.9	0.0	0.4
Grevillea robusta	1	21.8	8.7	0.9	0.9	0.0	0.4
Cocos nucifera	1	16.7	8.9	0.9	0.9	0.0	0.4
Manilkara bidentata	1	16.5	7.5	0.9	0.9	0.0	0.4
Psidium guajava	2	10.9 (0.77)	4.4	1.9	0.9	0.0	0.4
Brassaia actinophylla	1	13.7	6.5	0.9	0.9	0.0	0.4
Crescentia cujete	1	11.7	7.3	0.9	0.9	0.0	0.4
Guaiacum officinale	2	7.8 (1.6)	3.1 (20)	1.9	0.9	0.0	0.4
Annona reticulata	1	8.9	5.7	0.9	0.9	0.0	0.4

Calophylum calaba (both native) and *Areca catechu* (introduced).

Swietenia mahagoni x macrophylla, or hybrid mahogany, continues to be the dominant species (Table 1), increasing in Importance Value: from 24.3 percent in 2007 to 25.4 percent. This is due to both an increase in basal area growth and new tree recruitment. The importance value of *Peltophorum pterocarpum* decreased significantly. This is because in the last study, most *Peltophorum pterocarpum* were wrongly identified, since most were actually *Pterocarpus indicus*. Consequently, the species *Pterocarpus indicus* passed on to be the second most important species. The Importance Values that proceed hybrid mahogany start at less than 8 percent. Ten species occupy the lowest Importance Value (0.4 percent).

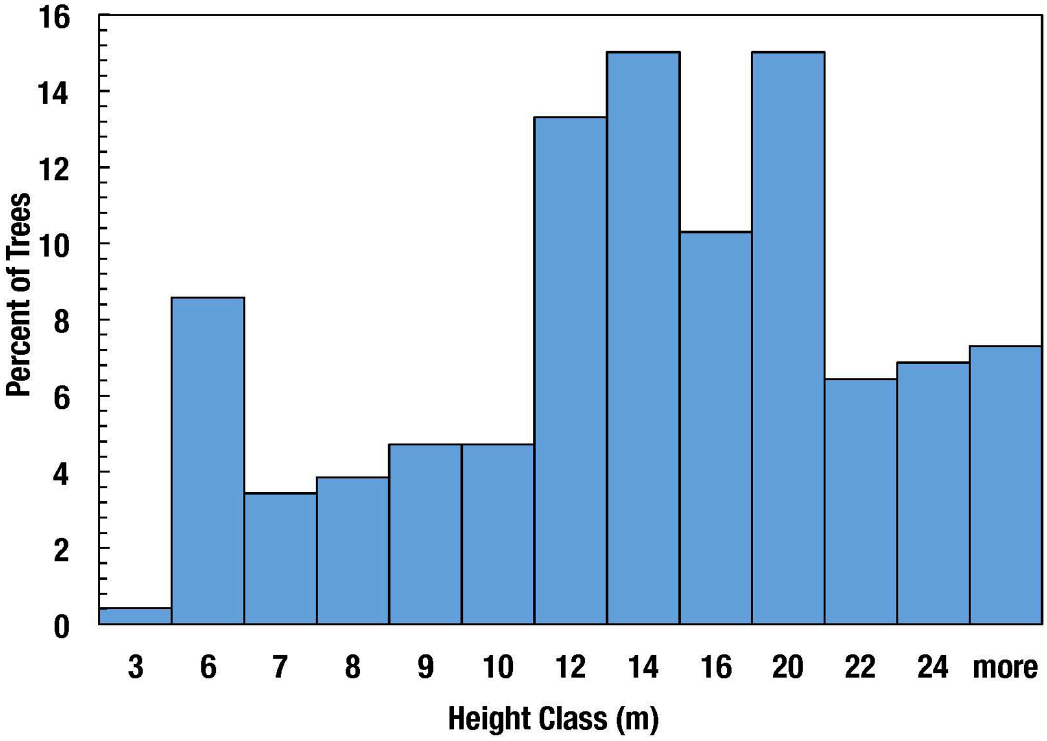
Structure

Trees in this forest had an average DBH of 31.5 cm (±1.5, n = 233), with 4.5 cm as the smallest DBH and 170 cm as the largest. When split into standardized classes, the 30 cm diameter group was the largest and 23.6 percent of the trees fell within this class (Fig. 3). With respect to height, the average tree was 14.5 m (±0.43, n = 233) in height. The largest tree was 30.2 m, almost twice the size of the largest tree in 2007 (16 m); the smallest tree was 1.8 m. The height classes with most individuals were the ones for 14 m and 20 m, both with 15 percent of all trees (Fig. 4). The average basal area was 1171.8 cm² (±137.4, n = 233).

We found 6 ingrowth trees that had established naturally, compared with what was found in 2007, where only one new t

FIGURE 3. Histogram of tree diameter at breast height classes.

Figure 4. Histogram of trees height classes.



ree was found. The rest of the new individuals were planted by residents and/or not taken into account in 2007. Some trees show decrease in height. The forest has a total basal area of 25.3 m²/ha; with an increase in 8 m²/ha since 2007 (17.3 m²/ha). The canopy has expanded and closed notably, when one compares an aerial photo from 2007 with one from 2015 (Fig. 5). However, the over-all distribution of the canopy has changed minimally. The number of stems per hectare continues to be larger than the amount of trees per hectare: 221 stems/ha vs. 136 trees/ha.

Growth and Mortality

The average growth rate in basal area was 49.5 cm²/yr (±6.5, n = 238). When grouped into standardized classes, 30.6 percent of the trees fell into the category of 10 cm² growth per year (Fig. 6). Eighteen percent of the trees fell into the category of 40 cm²/yr. and 4 percent of the trees fell in the >320 cm²/yr basal area growth category.

The trees grew an average height of 0.75 m/yr (±0.04, n = 238). Seventeen percent of the trees grew at a rate of 0.4 m/yr (Fig. 7). The tree with the highest growth rate did so at 6.2 m/yr. Meanwhile, a tree had a negative growth rate (-2.9 m/yr). We found a total of 25 dead stems. Some trees had not died, but some of their stems did; 10 trees died. The average mortality rate was 3 stems per year or 1.43 percent mortality/yr·ha.

Biomasss and Carbon Sequestration

The estimated aboveground biomass was 232 Mg/ha. For 2007, the total biomass calculated was 94 Mg/ha, which shows

Figure 5. Comparison of aerial photo of the Dr. Julio Víctor Rivera urban forest in El Paraíso Urbanization in 2007 and 2015 to highlight the visible change in growth. Both pictures taken using Google Maps (maps.google.com).

Figure 6. Histogram of basal area growth of trees measured at three time periods.

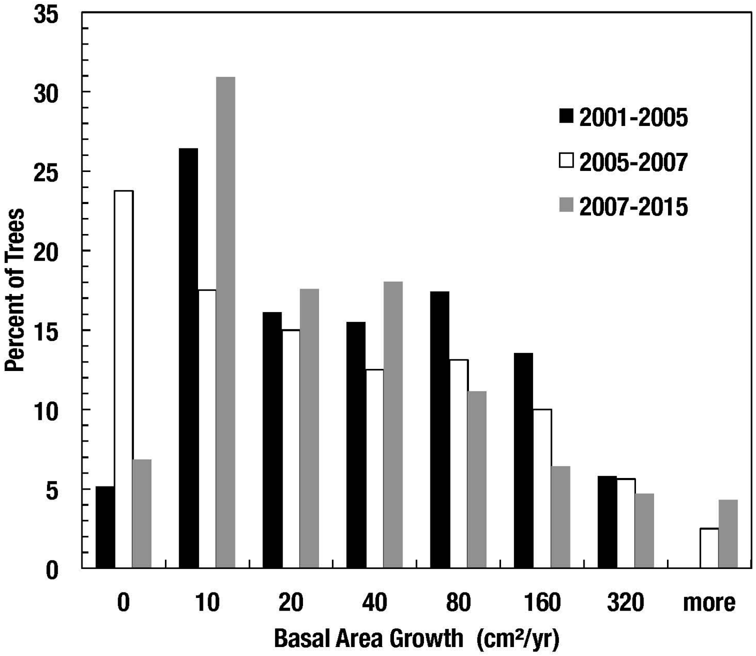
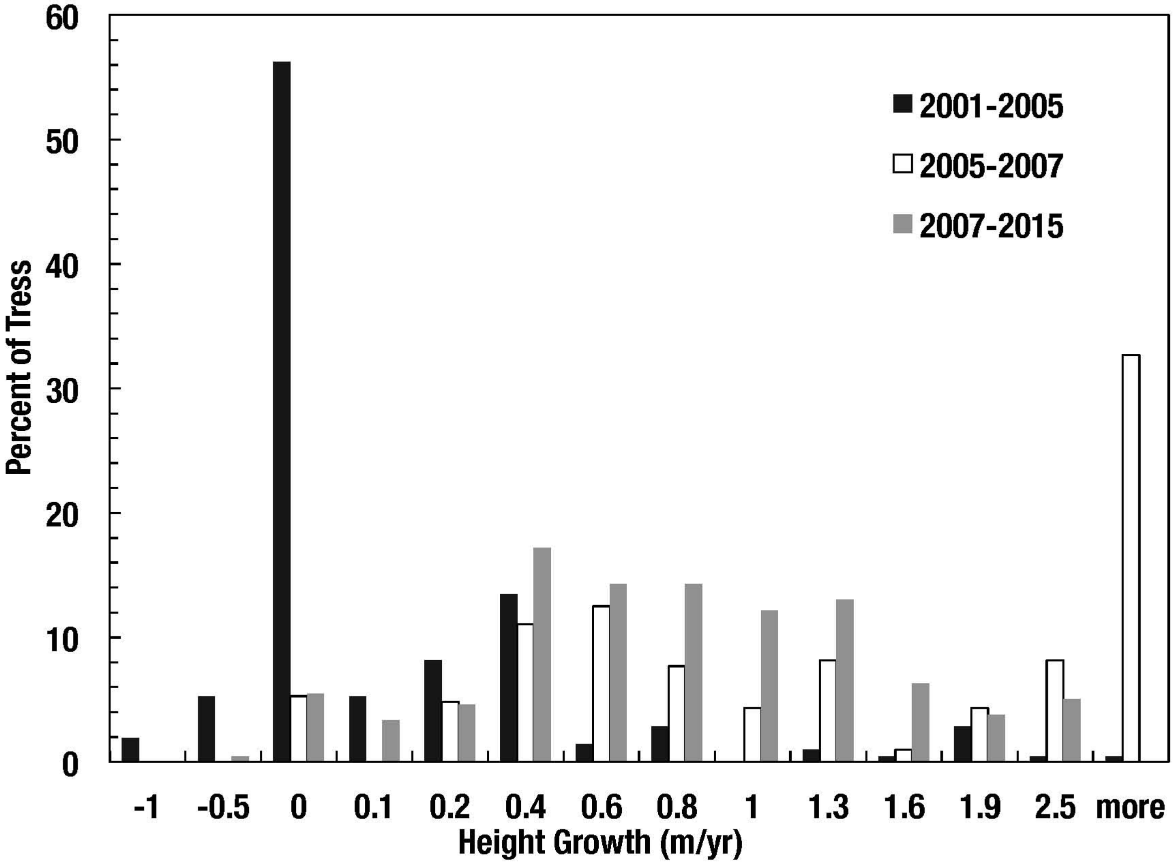


Figure 7. Histogram of height growth the trees measured at three time periods.



an increase of 18 Mg/yr.ha. Assuming that half of the biomass is composed of carbon, we estimated a 9 Mg/yr.ha carbon sequestration.

DISCUSSION

We found new trees that had established without being planted, which means that the forest has the potential to regenerate despite the constant intervention of the residents of the community. By finding new species we conclude that this forest has the capacity of diversifying. Both new native species that we found were trees that had established naturally. Native species could be establishing naturally because soil conditions could have slowly improved over time or perhaps as a result of canopy closure. Earlier, mostly introduced species adapted to open conditions prospered (Brown and Lugo 1994). This forest continues to have a unique composition of trees reflecting the preferences of the residents and managers of this urban forest, however with new individuals that, one way or another, achieved to establish naturally in spite of human activity.

The growth rates of all three periods of study (2001-2005, 2005-2007, 2007-2015) vary among themselves F(2,651) = 133.2, $p<0.001$ for height; F(2,651) = 15.7, $p<0.001$ for basal area (Figs. 8 and 9). During the 2005-2007 period, the forest underwent an accelerated rate of growth compared to the 2001-2005 and the 2007-2015 periods. These two lastly mentioned periods have similar values, for which they could represent a normal growth

Figure 8. Histogram of average tree height growth rates during the three time periods. The vertical lines represent the standard error of the mean (n = 238).

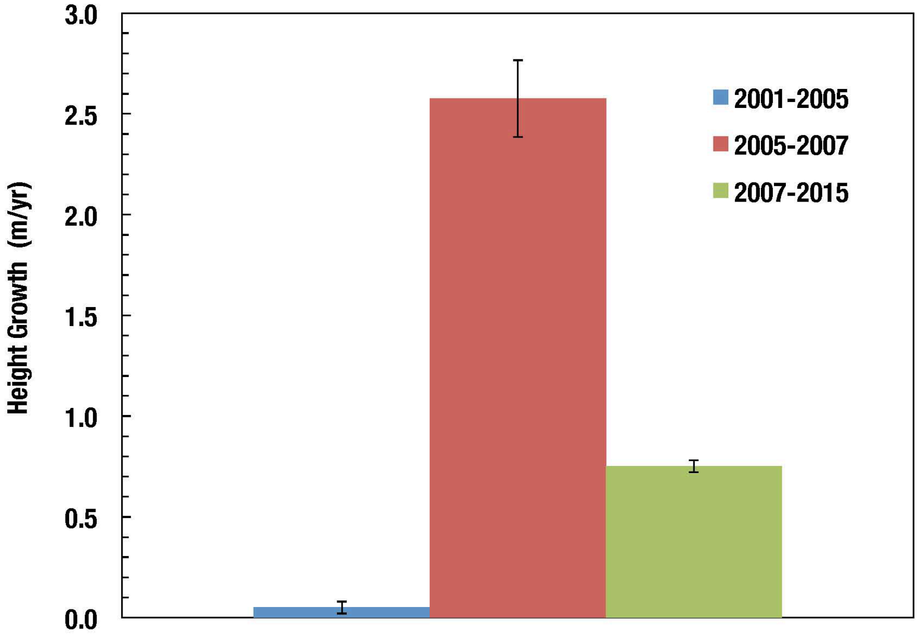
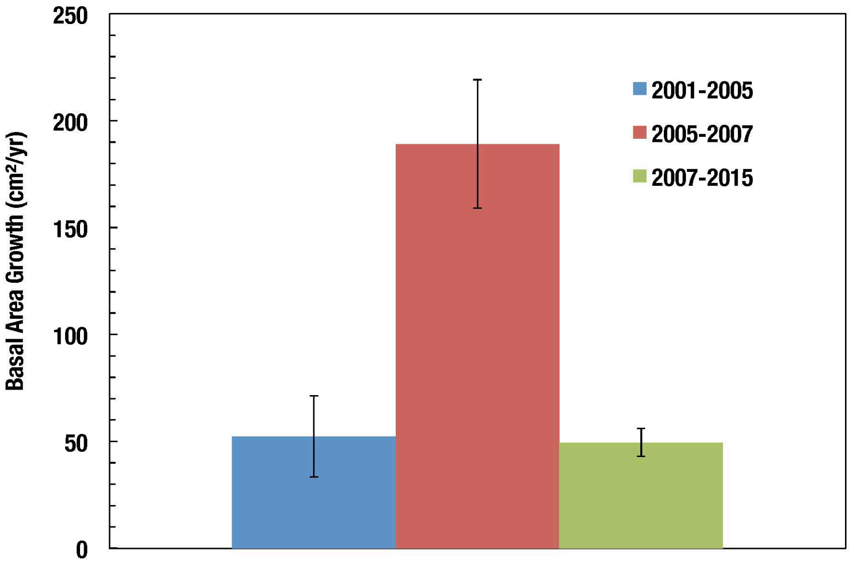


Figure 9. Histogram of average tree basal area growth rates during the three time periods. The vertical lines represent the standard error of the mean (n = 238).

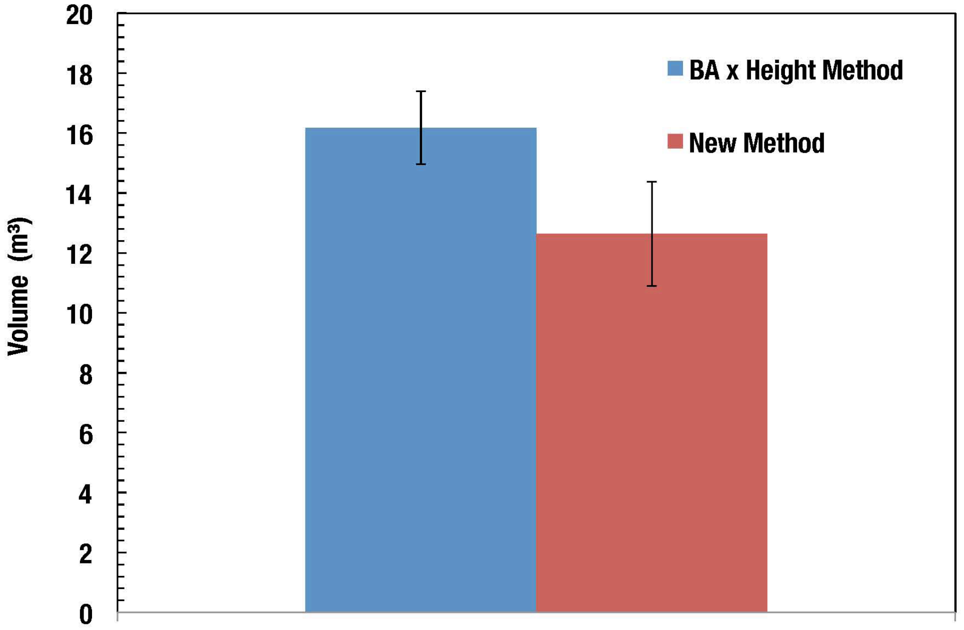


of the forest, while the 2005-2007 period could represent a growth burst due to multiple factors and environmental variables. We looked for the average rainfall per year for each period as a possible explanation of the growth pattern. Between 2001-2005, the average annual rainfall was 137 cm; between 2005-2007, the average annual rainfall was 168 cm and between 2007-20015 it was 175 cm (data from ncdc.noaa.gov) average rainfall increase by period was contrary to the growth rates; therefore, we cannot establish that rainfall was a determinant factor in the growth rates of the forest. More long-term monitoring could clarify the rhythm of the normal growth rates of this forest. During these periods no hurricanes passed through the country for which we can attribute this growth burst. But in 1998, Hurricane Georges affected the forest and the peak growth of 2005-2007 could be a delayed response to that event.

The estimation of carbon sequestration undertaken by this forest highlights the contribution of these urban forests to atmospheric carbon sequestration. Even though urban forests sequester less carbon than natural forests (Nowak and Crane 2002, Nowak et al. 2013), the estimation we made shows a large contribution of this small forest as opposed to no vegetation or pasture.

There was a difference in the tree volume calculated using our new method of estimation, however not statistically significant ($p>0.05$) (Fig. 10). Nowak (1994) cut trees in urban forests growing in more open spaces (open-grown) and shredded and measured their biomass manually and found that these trees had 80 percent of the volume compared to the volume obtained using allometric equations for natural forests

Figure 10. Histogram of the volume of four trees measured using our new method vs. the volume of those same trees using the traditional method for trees in natural forests (product between tree basal area and height). The lines represent standard error of the mean ($n = 4$).



(product of tree basal area and height). Even though the methods we used were not the same as Nowak's, and his study was done in a temperate region, more in depth study could help confirm if this adjustment of approximately 80 percent is applicable for measuring tree volume in urban forests in Puerto Rico and the rest of the tropics.

Besides its size, and considering Puerto Rico's forest cover, this forest, like other urban forests, has high ecological value since it supports forest communities, it can serve as a seed source for the regenera-tion of adjacent communities and spaces, and contributes to the reversion of the effects of deforestation (Lugo and Helmer 2004). Additionally, it serves as habitat for multiple animal species, including endemic ones (personal observation). The annual carbon sequestration that this forest performs increases its ecological value. These findings can highlight the importance of urban forests, providing information about their management, and can serve as a model and guide for the establishment of new urban forests in spaces with similar history as the Urban Forest of El Paraíso Urbanization in Río Piedras, Puerto Rico.

ACKNOWLEDGEMENTS

We thank Iván Vicéns for providing assistance in the field; the Natural Resources Career Tracks Program of the Department of Environmental Sciences at the University of Puerto Rico, Río Piedras Campus (UPRRP) for providing funding. This study was done in collaboration between the University of Puerto Rico and the International Institute of Tropical Forestry. We also thank Dr. David Ackerman and Dr. Frank Axelrod at the UPRRP Herbarium for helping identify and confirm a few of the species in the forest.

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JOBOS BAY MANGROVES REVISITED: GAS EXCHANGE, SALINITY, AND NUTRIENT RELATIONS

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ABSTRACT

We report results of an ecophysiological characterization of three mangrove species (*Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle*) and a mangrove associated species (*Thespesia populnea*) co-occurring at the Jobos Bay National Estuarine Research Reserve in Aguirre, Puerto Rico. The study was conducted in the summer of 2009 and included environmental measurements during a two-week period, sampling for leaf dimensional analysis, and determinations of leaf sap osmolality, gas exchange, and elemental composition (C, N, S, P, Na, K, Al, Ca, Mg, Mn, and Fe). Adult leaves of *Thespesia* were the largest (35 cm^2) and lightest (0.23 g), and *Rhizophora* had the heaviest (0.61 g) and second largest leaves (31 cm^2). The smallest leaf areas were recorded for *Laguncularia* (18 cm^2) and *Avicennia* (15 cm^2). The leaf area/weight ratio was high in *Thespesia* (149 cm^2/g), whereas mangrove species ranged from 52 to 60 cm^2/g. Mangrove leaves were rather succulent. The largest average values were measured in *L. racemosa* (42 mg/cm^2), while values of *Thespesia* were about one half of those of mangrove leaves. *Avicennia* leaves had the highest concentrations of N, S, P, K, Mg, and Mn, whereas *Laguncularia* showed the highest concentrations of Al, Ca, and percent of Ash. Concentrations of N and P, and those of Ca and Al, were positively correlated for all species. Leaf sap osmolality (mmol/kg) followed the sequence *Avicennia* (3140), *Laguncularia* (1769), *Rhizophora* (1696), *Thespesia* (1273). *Rhizophora* had consistently higher photosythetic rates and stomatal conductances but *Laguncularia* had the highest values of water use efficiency. Comparison with previous ecophysiological analyses in the same area, indicate more stressful conditions during the present study, as evidenced by the lower values of photosynthesis and leaf conductances.

Keywords: elemental composition, mangroves, osmolality, photosynthesis, salinity.

INTRODUCTION

The mangrove forests at Jobos Bay in Puerto Rico constitute a preferred area for ecological studies as they are legally protected as a national estuarine research reserve (Field 2002). The ecophysiological characterization of the mangrove species in the reserve was conducted during the late 90s in a study that analyzed the performance of three mangrove species along gradients of interstitial soil salinity including leaf gas exchange and leaf properties (nutrients and osmolality), and the analysis of nutrient cycling within fringe mangrove communities (Lugo et al. 2007). The present study reanalyzed the salinity and nutrient relations, in conjunction with an assessment of the relationships between leaf properties and photosynthesis of mangrove tree species. The study was carried out within the framework of a training course for high school students (see Acknowledgments).

The objective was to identify differences between mangrove species based on leaf morphology, leaf sap osmolality, and nutrient concentration, together with measurements of gas exchange. Also, we studied a transect including mangrove species and a presumably non-halophytic tree growing on soils at the interface between the back of mangrove communities and the beach, not flooded by seawater but exposed to salt spray. This study included leaf dimensions, osmolality and ionic composition of leaf sap, element concentration, and photosynthetic capacity. The results will be contrasted with a previous study conducted during a strong dry season several years before (Lugo et al. 2007).

MATERIALS AND METHODS

Measurements were carried out in the area of Camino de los Indios within the Jobos Bay National Estuarine Research Reserve (JOBANERR, Aguirre, Puerto Rico) (Fig. 1) during the 2nd and 3rd weeks of July 2009. Trees selected for analysis grew as part of the fringe mangrove vegetation dominated by *Rhizophora mangle* L. with *Laguncularia racemosa* (L.) Gaertn. f. as secondary species (A site in Fig. 1), and trees of *Avicennia germinan*s (L.) L. bordering the interior lagoon (B site in Fig. 1). For the sake of comparison with a presumably non-halophytic tree, specimens of *Thespesia populnea* (L.) Sol. ex Correa were also sampled during the 3rd week. These trees were found on sandy soils, beyond the reach of tides, behind the mangrove fringe.

From now on the species will be designated only by the genus name. The trees selected were growing approximately within the same area studied in 1998 by Lugo et al. (2007).

Environmental Measurements

Climate parameters (rainfall, temperature, relative humidity, and photosyntetically active radiation) were recorded at 15 minutes intervals by the automatic meteorological station of JOBANERR.Temperature and humidity, and air CO_2 concentrations were also measured outside and below the canopy of a mangrove fringe using a Vaisala MI70 recorder with Humidicap and Carbocap sensors.

Interstitial and surface water was sampled to measure salinity *in situ* (refractometer), osmolality in the JOBANERR laboratory (Wescor osmometer), and ion concentrations at the International Institute of Tropical Forestry laboratory in Río Piedras, using Inductively Coupled Plasma spectrometry (ICP).

Piezometers were located about 30 cm depth within areas rooted by *Rhizophora* and *Avicennia* to determine potential changes in salt concentration of interstitial water. Samples were also taken from piezometers located in an area devoid of mangrove roots at the bay near the coastline.

Leaf Properties

Healthy leaves of different age, differentiated by their position in the shoot as young, adult, and old, were collected into plastic bags, and stored in dark coolers for transportation to the laboratory, where leaf area and fresh mass were measured upon arrival. The most practical procedure to determine leaf area is the use of an optical planimeter, if it is not available leaf area can be easily determined drawing the leaf on paper and then cutting and weighing the shape.

Paper shapes of known area are used to calibrate the weight-area relationship. If it is necessary to measure leaf area in the field without severing the leaf, the use of allometric relationships is appropriate. During the field course 50 adult leaves per mangrove species were collected, and their maximum dimensions of length and width were measured. The product length x width was regressed against leaf area measured using the drawing technique.

Leaves were ovendried at 65º C for 24 hours, and weighted again (dry mass). With these values we calculated the specific leaf area (SLA) (leaf area/leaf dry mass), the leaf water content (fresh mass – dry mass) and succulence (leaf water content/leaf area).

Leaf sub-samples were stored in plastic syringes and frozen in dry ice. After 24 hours syringes were thawed in the lab counter and squeezed with a hand press to extract leaf sap, on which osmolality and ionic composition were measured using the methods mentioned above.

Samples of adult leaves were dried in a ventilated oven at 65º C, grinded, and ashed at 490º C. Ashes were dissolved in HCl 1N. Concentrations of Na, Mg, Al, P, S, K, Ca, Mn, and Fe were measured by ICP. The S concentration measured corresponds only to the inorganic S fraction, as organic S is certainly lost during ashing as SO_2. Carbon and N were measured with a Leco elemental analyzer. All concentrations except of % Ash are expressed in mmol/kg dry mass for direct interelemental comparisons.

Gas exchange (CO_2 and H_2O) was measured with an infrared gas analyzer (LCPro, ADC). Measurements were conducted from early morning to early afternoon (ca. 8 am to 1 pm). The gas analyzer records differential of CO_2 and water vapor concentrations (vpm) between the air surrounding the leaf and the air passing through the leaf chamber at constant airflow rates. In addition, intensity of incoming radiation (μmol $m^{-2}s^{-1}$) and leaf temperature (ºC) are recorded simultaneosly. Rates of following processes are calculated with these parameters:

1. Rates of net of CO_2 uptake (photosynthesis A) or production (respiration R) (μmol $m^{-2}s^{-1}$)
2. Stomatal conductance (gs) (mmol $m^{-2}s^{-1}$) and rate of transpiration (E) (mmol $m^{-2}s^{-1}$)
3. Water use efficiency calculated either as the quotient between net photosynthesis and transpiration (A/E), or as the quotient A/gs (intrinsic water use efficiency) (μmol/mmol).

Statistical Analyses

Data were submitted to analyses of variance and regression using the JMP 8.0 statistical package (SAS).

FIGURE 1. Study site: Camino de los Indios, Jobos Bay, Guayama, PR. The blue line indicates the location of the wooden path within the fringe mangrove. Imagery date: 11/1/2006. Lat 17.935437º long -66.253300º elev 0 m eye alt 298 m *Main camp; A Fringe site (*R. mangle* + *L. racemosa*; B Basin site (*A. germinans*); C Bank site (*Thespesia populnea*)

RESULTS

Environmental Conditions

The climate parameters recorded during the month of July indicated rainfall only at the beginning (about 9 mm during the first 2 days of the month). Temperature ranged from a minimum average of 25 to 27° C (except in days 15th and 17th when minimum temperatures were 23° C) and maxima surpassing 30° C except in days 16 and 27. Relative humidity followed the expected opposite pattern with maxima between 70 and 90 percent in the night and minima around 54 percent, except day 21st (minimum at 40 percent). The pattern of the sum of PAR during the measuring period indicates that most days received a little more than 30 moles quanta m^{-2} day^{-1}. During cloudy days (20nd and 21st day) PAR decreased dramatically.

During sunny days maximum temperatures outside the vegetation approached 35º C and minimum temperatures were between 25 and 27º C. In the understory of a forest plot dominated by *Rhizophora,* maximum temperatures were nearly 2º C lower, but minimum temperatures were less than a 1º C lower. The relative humidity followed an opposite pattern, maximum values being recorded near the end of the night varying in three nights between 77 and 84 percent. Minimum humidities recorded about 2 hours after noon, were lower outside and varied between 56 and 50 percent.

The Vaisala CO_2 probe was set up only in the understory of the *Rhizophora* plot to evaluate levels and variability of CO_2 concentrations. Carbon dioxide concentrations in the understory measured at 1-minute intervals varied strongly throughout the measuring period. The 4-minute moving average showed minimum values of 380 ppm measured near the end of the light period, and 480 ppm measured at the end of the night period.

Leaf Characteristics

The regression lines for the product length x width were quite similar and provided a good estimation of leaf area (Fig. 2). The three species followed similar linear relationships indicating a common leaf shape. However, the slope of the regression lines increased slightly but significantly from *Rhizophora* to *Avicennia* and *Laguncularia*. In this data set, average leaf area (cm^2) was greater for *Rhizophora* (38.8 ± 6.7), and smaller for *Laguncularia* (17.6 ± 4.3) and *Avicennia* (15.5 ± 3.7).

Leaf Dry Mass and Area

The leaves of *Rhizophora* and *Avicennia* followed broadly the same weight-area relationship (Fig. 3). Leaves of *Laguncularia* showed a tendency to develop heavier leaves per unit area, whereas *Thespesia* showed the opposite tendency (Fig. 3). Discrimination of leaf groups by age and species revealed that *Rhizophora*, *Avicennia,* and *Thespesia* increased both dry mass and area from the young to the adult stage remaining similar at the old stage, whereas in *Laguncularia* both parameters continued to increase into the group of old leaves (Fig. 4A, B).

Leaf succulence remained similar for all age groups in *Avicennia* and *Thespesia*, increased slightly with age in *Rhizophora*, whereas in the case of *Laguncularia* succulence increased significantly from young to adult and old leaves (Fig. 4C). Leaf area/mass ratios of the mangrove species decreased slightly, whereas *Thespesia* increased slightly, as the leaves age (Fig. 4D).

Composition and Osmolality of Interstitial Water and Leaf Sap

Measurements of interstitial water salinity during two consecutive weeks showed that there was a small but consistent tendency for interstitial water obtained from within red mangrove roots to be more concentrated (higher values of salinity, conductivity, and osmolality) than the water samples obtained from root-free sites (Table 1). Average interstitial water from sites occupied by *Avicennia* was much more concentrated than the average of *Rhizophora* sites. A comparable site free of *Avicennia* roots was not available. In the *Avicennia* site, salinity values were lower during the 2nd week, whereas those of the *Rhizophora* site increased slightly.

The osmolality of leaf sap from the species studied confirmed that *Avicennia* is usually the species with higher leaf sap osmolality followed by *Laguncularia* and *Rhizophora* (Fig. 5). *Thespesia* showed the lowest osmolality values.

FIGURE 2. Regression of the product of length x width of mangrove leaves vs actual leaf area. *Rhizophora mangle* (red)(n=49) A cm^2 = 4.42793 + 0.62559 * (L x A); R^2 Adj: 0.94 L*aguncularia racemosa* (green)(n=50) A cm^2 = -0.73106 + 0.79375 * (L x A); R^2 Adj: 0.92 *Avicennia germinans* (black)(n=50) A cm^2 = 0.76645 + 0.66201 * (L x A); R^2 Adj: 0.93

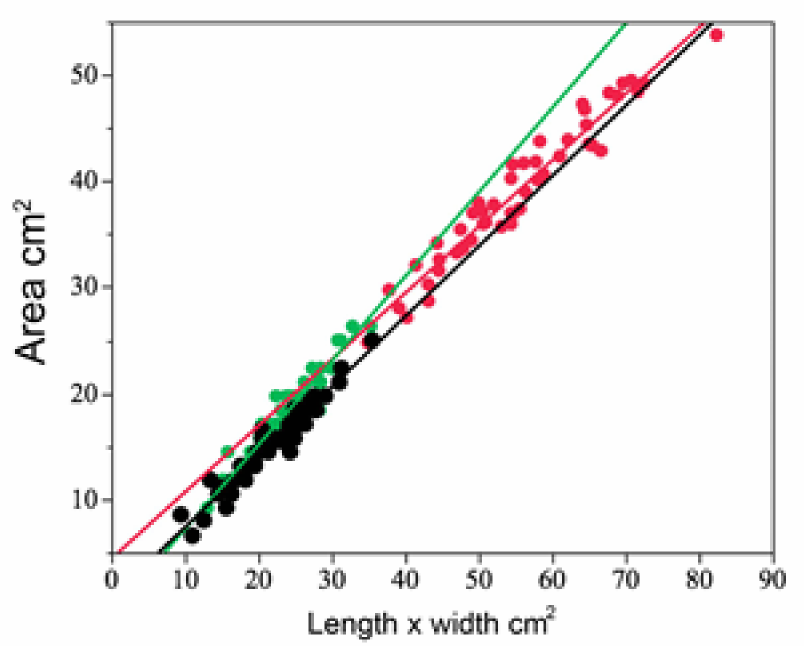


FIGURE 3. Area/mass relationship of different species from tree species at Jobos Bay. The regression equations are: Area (A cm^2) and mass (W g)
Thespesia (blue) A= 5.615 +111.890 W; R^2adj=0.87; F=927, P>F <0.0001; n= 146
Avicennia (black) A= 3.235 +43.358 W; R^2adj= 0.75; F=893, P>F < 0.0001; n=299
Rhizophora (red) A= 4.857 +41.599 W; R^2adj= 0.89; F= 2436, P>F <0.0001; n=297
Laguncularia (green) A= 7.146 +24.772 W; R^2adj= 0.68; F= 321, P>F <0.0001; n=149

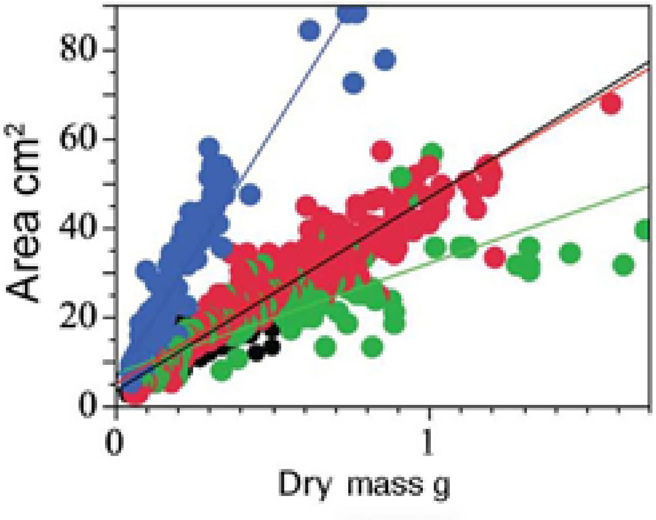


Figure 4. Comparison of means of leaf dry weight (A), area (B), succulence (C) and area/weight ratio (D) using analysis of variance, and an a posteriori test (Tukey-Cramer Honest Significant Difference). Black dots: *Avicennia*; Green dots: *Laguncularia*; Red dots: *Rhizophora*. Y: young leaves; A: adult leaves; O: old leaves. The green diamonds depict the result of the analysis of variance. Overlapping diamonds indicate that the means are statistically identical at P≤ 0.01.

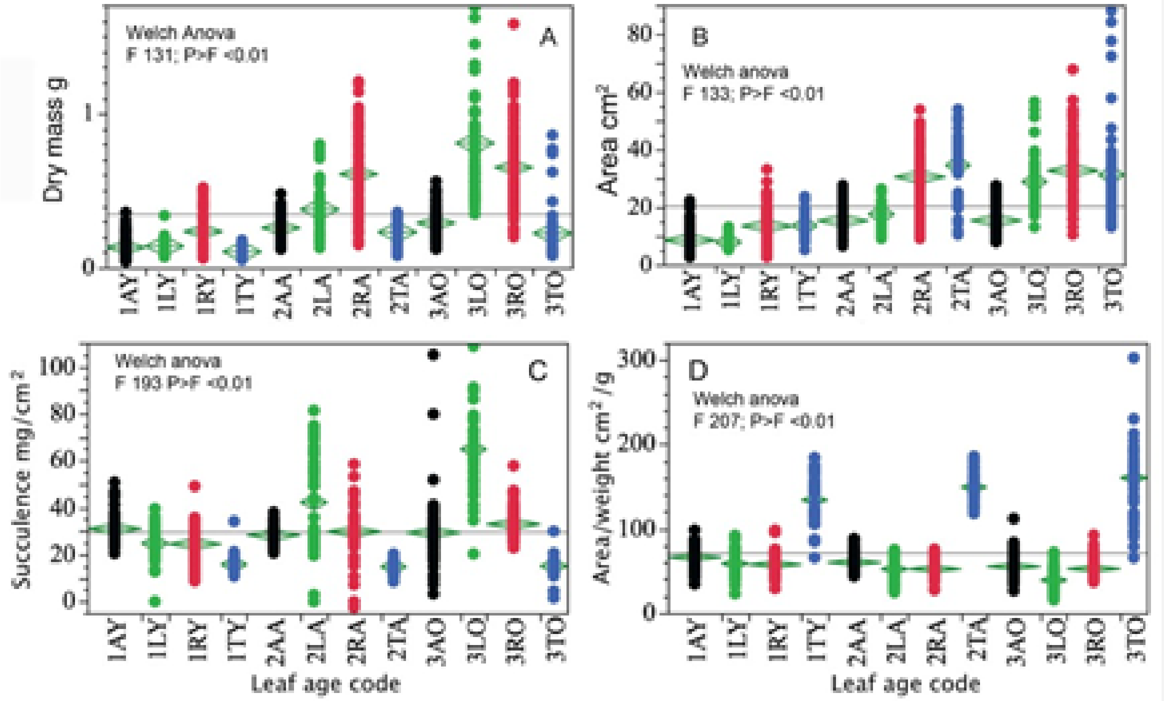


Table 1. Salinity of interstitial water collected from piezometers at 30 cm depth (mean ± standard deviation)

Site and time measurement	n	Salinity %	Conductivity µS	Osmolality mmo/kg
July 13 (11:00; 11:30; 14:00)				
Rhizophora site				
Outside roots	3	39 (2)	58 (0)	1099 (3)
Inside roots	3	43 (1)	60 (3)	1147 (15)
Avicennia site	3	92 (1)	120 (1)	2831 (38)
July 20 (11:00; 11:30; 14:00)				
Rhizophora site				
Outside roots	3	42 (1)	59 (0)	1274 (245)
Inside roots	3	55 (1)	75 (0)	1499 (4)
Avicennia site	3	59 (2)	80 (2)	1632 (48)

Analysis of the elemental composition of leaf sap from adult leaves of the mangrove species revealed interspecific differences in the nutritional requirements (Table 2). Compared to standard sea water (DOE 1997) the element concentration in leaf sap gave following ratios: K was 11, 13, and 7 times higher in *Avicennia*, *Laguncularia,* and *Rhizophora*, respectively; Ca was slightly lower in *Avicennia*, 7 times higher in *Laguncularia* and nearly 5 times higher in *Rhizophora*; Mg was 3, 2, and 1.5 times higher in *Avicennia, Laguncularia,* and *Rhizophora* respectively; Na was twice as high in *Avicennia*, 0.8 times in *Laguncularia* and *Rhizophora;* S was 4, 2, and 3 times higher in *Avicennia, Laguncularia,* and *Rhizophora* respectively.

Nutrient Concentration of Adult Leaves

Avicennia leaves stand out for their higher concentrations of N, S, and P. *Laguncularia* and *Rhizophora* leaves showed similar values of Na and S, but lower C concentration than the other two species (Table 3). *Avicennia* stands out again due to the significantly higher concentrations of K, Mg, and Mn, whereas *Laguncularia* showed the largest values of Al, Ca, and of %Ash (Table 3). As expected, the %Ash was linearly correlated with the ∑cations (%Ash= 1.66038 + 0.00429 * ∑cations; R^2= 0.95), and Na was the main ion responsible of this high correlation (%Ash= 5.28766 + 0.00473 * Na; R^2= 0.72). The usual high level of correlation between Ca and %Ash did not apply due to the reduced Ca uptake by *Avicennia.* The Ca concentrations in all species appeared to be correlated with the concentration of Al. The two extremes of the correlation are *Avicennia*, with low Ca and Al concentrations, and *Laguncularia*, with high Ca and Al concentrations.

Thespesia differed strongly from the mangrove species for its high concentrations of N and P (Table 4). In addition, *Thespesia* showed significantly lower Na and higher K concentrations within the group of species studied. These results point to the non-halophytic character of *Thespesia.*

Gas Exchange and Water Use Efficiency

We found a linear relationship between leaf conductance and net assimilation, and between transpiration and net assimilation for all the mangrove species combined (Fig. 6). The averages of photosynthesis, transpiration, and leaf conductance of adult leaves at light intensities above 900 µmol $m^{-2}s^{-1}$ were higher for *Rhizophora* compared to the leaves of the other mangrove species (Table 5). These rates were attained at leaf temperatures around 38ºC. Calculated water use efficiency (A/E) was also higher in *Rhizophora*, but intrinsic water use efficiency (A/gs) was similar for *Rhizophora* and *Laguncularia* (Fig. 7). Both ratios were lower for *Avicennia*, the species that generally occupies the most saline, and at times, drier locations in mangroves along semiarid coastlines.

DISCUSSION

Environmental conditions experienced during the measuring period exemplify the high radiation and temperature stress to which mangroves in the Caribbean are submitted during summer months. These stress factors compound the effect of interstitial water salinity derived from seawater moved diurnally by high tides. Mechanisms to tolerate this stressful environmental conditions are well known. They include adaptations of the photochemical apparatus in mangrove leaves for avoiding photoinhibition through several pathways of photochemical and non-photochemical quenching (Naidoo et al. 2002, Thomas et al. 2009); regulation of leaf temperature and evapotranspiration by high levels of leaf inclination reducing

Figure 5. Osmometry of leaf sap obtained from adult leaves. The green diamonds correspond to the visual representation of the one-way analysis of variance performed by JMP. Black dots: *Avicennia*; Green dots: *Laguncularia*; Red dots: *Rhizophora*. Y: young leaves; A: adult leaves; O: old leaves. Significance of the green diamonds as in Fig 3.

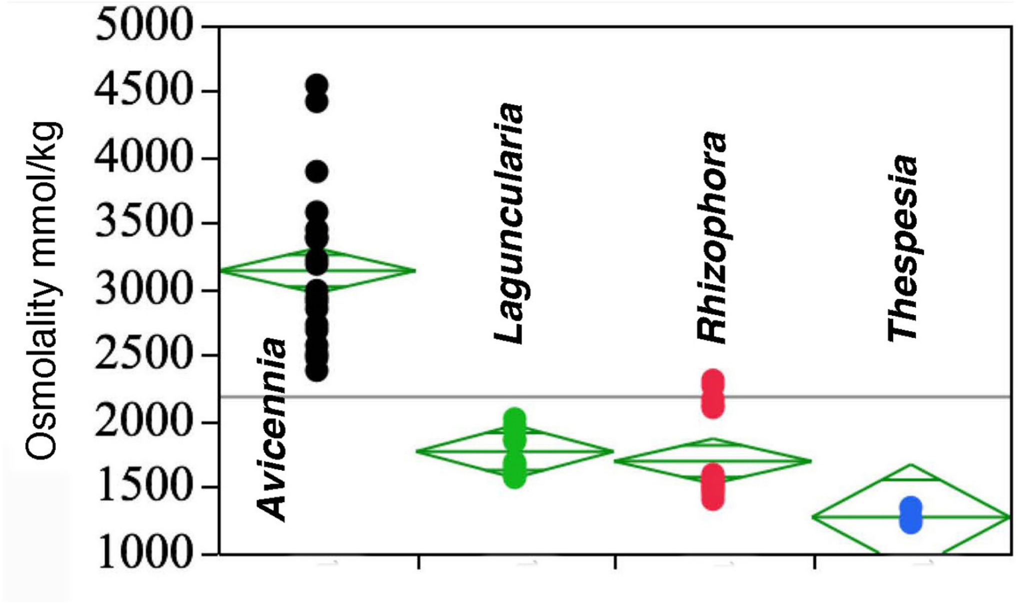


Table 2. Ion concentration (mmol/kg)(standard deviation) in insterstitial water and leaf sap extracted from adult leaves.

	n	Ca	K	Mg	Na	P	S
Standard seawater	-	10	10	53	486	-	29
Interstitial water no roots	2	16	5	41	500	0.0	38
Interstitial water with *Rhizophora* roots	2	12	4	41	509	0.0	37
Interstitial water w. *Avicennia* roots	2	45	107	107	993	0.0	95
	Leaf sap Mean (standard deviation)						
Avicennia germinans	8	7 (4)	111 (28)	144 (32)	1022 (219)	4.8 (1)	124 (18)
Laguncularia racemosa	8	70 (28)	128 (15)	83 (7)	395 (28)	5.1 (2.3)	45 (8)
Rhizophora mangle	8	47 (19)	70 (14)	117 (36)	408 (193)	2.9 (0.9)	84 (47)

TABLE 3. Average elemental composition of adults leaves of mangroves at Jobos Bay (July 2009). Means followed by the same letter are not statistically different (Tukey-Kramer HSD test, P=0.05). N= 10

Non-metallic elements	C mol/kg	N	S	P
		---------------------	mmol/kg	---------------------
Avicennia	38.5a	1040a	268a	45a
Laguncularia	32.6b	588b	173b	32b
Rhizophora	39.2a	659b	158b	37ab

Metallic elements	Na	K	Mg	Al	Ca	Mn	Fe	∑cation	%Ash
	------------	------------	------------	------------	mmol/kg	------------	------------	------------	------------
Avicennia	2217a	503a	784a	3.6b	257c	3.5a	1.1a	3267a	15.4b
Laguncularia	2227a	311b	500b	13.8a	1117a	0.8c	0.8ab	3920a	19.3a
Rhizophora	1147b	322b	400b	4.8b	535b	2.5b	0.7c	2091b	11.0c

TABLE 4. Average element concentrations (mean ± standard deviation) in adult leaves of *Thespesia populnea* compared to the mangrove species growing nearby.

Species	n	C mol/kg	N	P
			-------mmol/kg	-------
Avicennia	9	37.2 (1.7)	1273 (87)	55.9 (4.5)
Laguncularia	4	32.0 (1.0)	544 (67)	29.2 (2.1)
Rhizophora	9	38.9 (2.8)	811 (78)	38.7 (3.9)
Thespesia	5	36.0 (0.8)	2191 (100)	98.2 (6.8)

Species	n	Na	K	Mg	Ca
		-------------------	-------mmol/kg	-------------------	-------------------
Avicennia	9	2073 (326)	759 (181)	684 (65)	187 (42)
Laguncularia	4	2427 (136)	262 (38)	657 (41)	1671 (132)
Rhizophora	9	1281 (600)	256 (97)	357 (135)	405 (147)
Thespesia	5	319 (33)	1263 (110)	358 (23)	1243 (57)

Figure 6. Relationship between leaf conductance (gs), transpiration (E), and CO_2 assimilation (A) recorded in leaves of mangroves in Jobos Bay, July 2009. Black dots: *Avicennia*; Green dots: *Laguncularia*; Red dots: *Rhizophora*. Y: young leaves; A: adult leaves; O: old leaves.

Significance of the green diamonds as in Fig 3. Overall regressions: A (mmol/m^2.s) = 1.2012 + 68.859 gs (mol/m^2.s); R^2adj= 0.871

A (mmol/m^2.s)= 0.882 + 3.130 E (mmol/m^2.s)

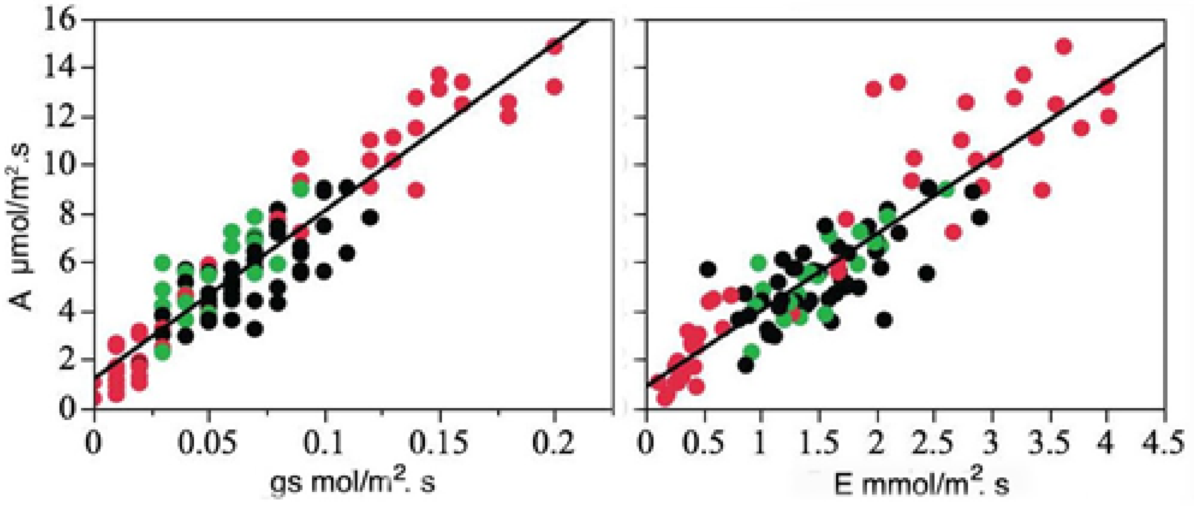


Table 5. Gas exchange parameters (95 percent confidence limits) of adult mangrove leaves exposed to light intensities ≥ 900 µmol m^{-2} s^{-1} measured in July 2009 in Jobos Bay, Aguirre, Puerto Rico.

	Rhizophora	*Laguncularia*	*Avicennia*
A (µmol m^{-2} s^{-1})	8.4 (6.7-10.1)	5.5 (4.8-6.3)	5.5 (4.7-6.3)
g_s (mmol m^{-2} s^{-1})	99 (74-119)	53 (44-61)	63 (53-73)
Intrinsic water use efficiency (µmol/mmol)	103	110	89
Q leaf (µmol m^{-2} s^{-1})	1242 (1163-1320)	1177 (1110-1243)	1253 (1181-1325)
T leaf (°C)	38.2 (37.6-38.8)	38.6 (38.1-39.2)	38.3 (38.0-38.7)

the total energy absorbed by the leaf (Ball et al. 1988); osmoregulation through the accumulation of ions in the vacuole that counteract osmotic effect of interstitial water salinity (Popp 1984, Medina and Francisco 1997, Paramita et al 2007); and organic molecules presumed to be accumulated in the cytoplasm (compatible solutes) (Popp et al. 1984; Medina et al. 1990).

The nutritional aspects associated to mangrove adaptations to salinity stress are also comparatively well known. It is generally accepted that mangrove communities, particularly mangrove fringes dominated by *Rhizophora mangle,* are frequently regulated by the availability of P, causing stunted growth and dwarfism (Feller 1995, Cheeseman and Lovelock 2004, Medina et al. 2010). However, N can also be limiting particularly in areas where water runoff and sediment supply are limited (Boto and Wellington 1983, McKee et al. 2002).

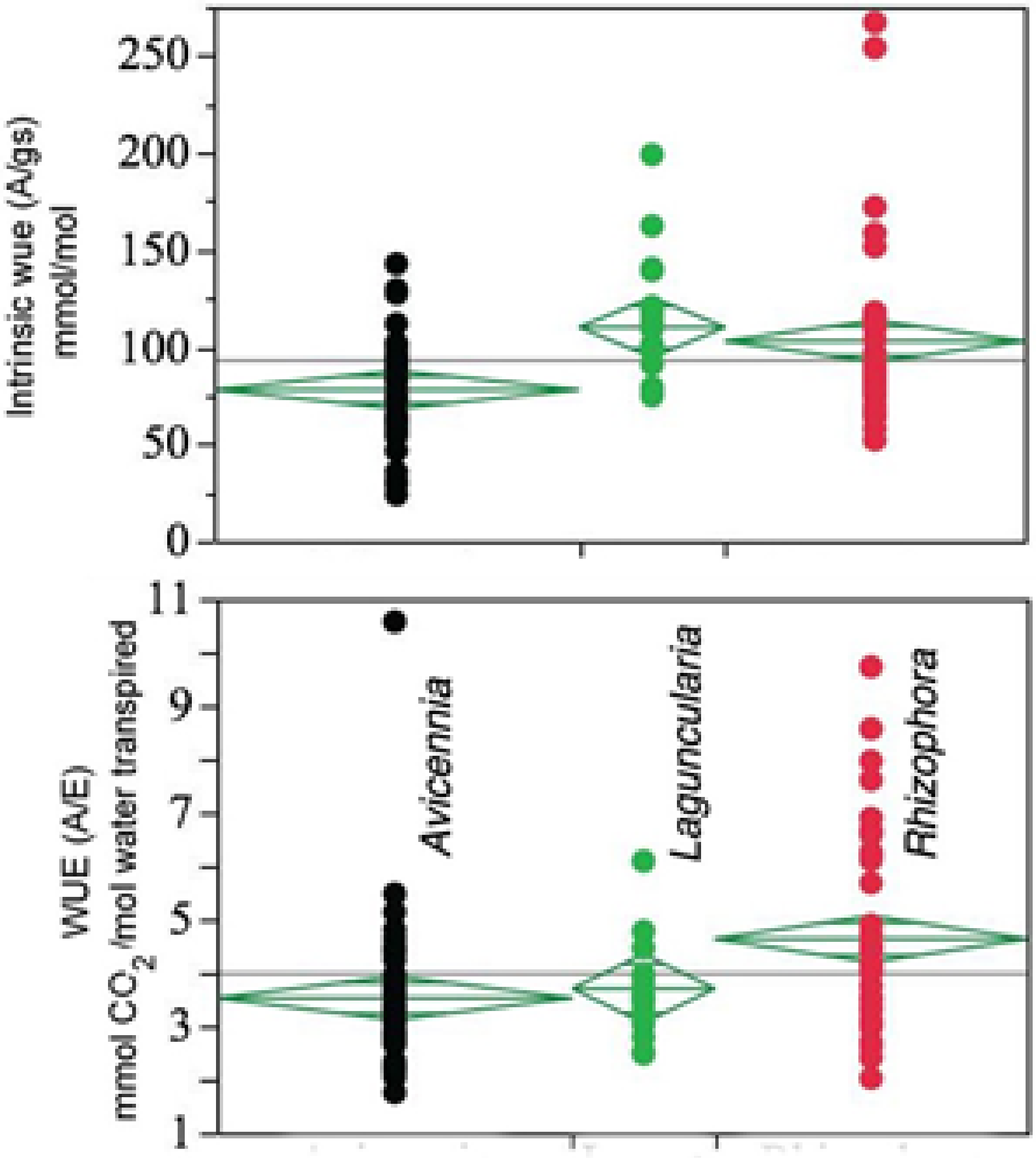
The elemental composition of mangroves has been investigated mostly with regards to the osmotic adaptations, but comparatively little is known about specific requirements of metallic elements and sulfur. The documented differences in elemental composition among mangrove species, does not have a comprehensive physiological explanation (Medina et al. 1990, 2007, Lugo et al. 2007). The recent review of Reef et al. (2010) deals mainly with N and P nutrition but the ecophysiological role of S is not mentioned. In fact, a thorough documentation of the ionome profile of mangrove species in the sense of Salt et al. (2008) is missing in the analysis of the ecophysiological relationships of these species.

Mangroves develop roots in saline soils. In the process of water and nutrient absorption from interstitial water ions such as Na and Cl are preferentially excluded resulting in increased salt concentration in the root environment (Passioura et al. 1992). As far as we know this statement has not been tested under field conditions. The process is probably more pronounced in species such as *R. mangle*, described as a salt excluder, than in *A. germinans*, a salt secreting species (Scholander 1968). Our results indicated that interstitial waters within *Rhizophora* roots had higher concentrations of Ca, Na, and S, but lower concentrations of K and Mg. Water within *Avicennia* roots showed a distinctive pattern with higher concentrations of Ca (4 times), K, Mg, and Na (≈ 2 times) than standard sea water. This pattern may be explained by evaporation in the *Avicennia* site that is not compensated by wave movement and tides as in the *Rhizophora* site.

The substantially higher concentration of Ca may also be related to the rejection of this ion by *Avicennia* roots. Results presented here must be considered preliminary, but support the assumption of accumulation of salt in the water surrounding the root system of *Rhizophora* trees. Detailed and extensive measurements of this type that account for the effect of tides in counteracting the concentration process may help improve our understanding of salt regulation in mangrove communities.

Laguncularia had the heaviest leaves per unit area among the mangrove species, whereas dry coastal forest species *Thespesia* had comparatively the lightest leaves per unit area. Adult *Rhizophora* leaves were always larger and heavier than leaves of the other species studied, in agreement with several other studies (Medina et al. 2007, Medina and Francisco 1999, Medeiros and Sampaio 2013). A gram of dry weight invested in leaves corresponds to 32 cm^2 in *Laguncularia*, about 46 cm^2 in *Avicennia* and *Rhizophora,* and 118 cm^2

Figure 7. Comparison of indices of water use-efficiency (wue): Intrinsic water use-efficiency= A/gs in mmol/mol; Water use-efficiency= A/E in mmol CO_2/ mol water transpired.



in *Thespesia*. These differences imply that investment of photosynthate and nutrients for building photosynthetic area may be relevant in determining the efficiency of organic matter production of these coastal communities.

Regarding succulence, the species studied were similar only at the young stage. At the adult and old stages *Laguncularia* leaves always had the highest, and *Thespesia* the lowest, water content per unit area. *Avicennia* and *Rhizophora* had similar succulence values at all leaf stages and, including *Thespesia,* this index did not increase from adult to old leaves. The implied mechanism of diluting excess salt in leaf tissues through parallel increased uptake of water may have implications for leaf demography in *Laguncularia.* A recent study showed that leaf life span of *L. racemosa* was 2 months shorter than that of *R. mangle* and about 6 months shorter than that of *A. schaueriana* (Medeiros and Sampaio 2013).

The consistently higher leaf sap osmolality in *Avicennia* may be associated with the higher permeability for salt in the roots of this species, and also by its occurrence in saltier sites. *Avicennia* has leaf salt glands that actively secrete salt throughout its lifetime and salt secretion rates increase with interstitial water salinity (Suárez and Medina 2008). *Laguncularia* also has leaf salt secreting glands (Sobrado 2004), but osmolality of leaf sap is much lower than that of *Avicennia* and similar to that of *Rhizophora*, a salt excluding mangrove (Scholander 1968). This may be the result of an increase in the water content per unit area induced by growth in saline environments (Biebl and Kinzel 1964), leading to similar leaf sap concentrations as in the salt excluding *Rhizophora*. The concentration of Na in leaf sap showed a pattern similar to osmolality among species, around 1000 mmol/kg in *Avicennia*, and 400 in *Laguncularia* and *Rhizophora*. But it is remarkable that *Laguncularia* and *Avicennia* have similar K concentrations, both significantly higher than those of *Rhizophora.* In addition, Ca is ten times more concentrated in *Laguncularia* compared to *Avicennia*, whereas S (as sulfate) is three times higher in *Avicennia* compared to *Laguncularia*. The physiological causes and implications of these ionic relationships are known only for the case of Ca. *Avicennia* is an “oxalate plant” sensu Kinzel (1989). The production of oxalic acid prevents the accumulation of soluble Ca in leaf sap.

Nutrient analyses of adult leaves essentially confirm results reported by Lugo et al. (2007). *Avicennia* showed the highest values for N, P, K, per dry mass and highest values of Na and lowest Ca values in leaf sap. The present paper reports also high concentrations of S and Mg compared to the other species. *Laguncularia* is the species with highest Ca concentration in contrast to the previous results. The Na/K ratios of the mangroves around the same range measured previously, varying between 7.2 in *Laguncularia* and 3.6 in *Rhizophora*. *Thespesia* trees on the other hand, stand out with much higher concentrations of N, P, K than those found in the mangrove species, and the Na/K ratio was only 0.25, a clear indication of the non-halophytic character of this species, and that it was not submitted to salt stress.

The present data set includes concentrations of Al, Mn, and Fe in adult leaves of mangroves trees. The former was always correlated with leaf Ca content, a relationship that was somewhat unexpected because of the inmmobilization of Al in soils as a consequence of pH increases brought about by presence of Ca carbonate. This is one of the research questions that should be addressed using cultivated plants.

Photosynthetic rates and indices of water use efficiencies expand previous findings in JOBANERR mangroves (Lugo et al. 2007). Photosynthesis was operating at intensities above 900 µmol m^{-2} s^{-1} and temperatures above 35º C, however, leaf conductances were below the 100 mmol $m^{-2}s^{-1}$ indicating a certaindegree of stomata closure. Results reported in this paper correspond to the middle of the summer in Puerto Rico (July), and to a certain extent contrast with previous reports from the same site that were obtained in the middle of the winter (December) (Table 6). Present data indicates that plant were under water stress, their leaf sap osmolalities were well above, and leaf conductances and photosynthetic rates were considerably below those reported from the same site by Lugo et al. (2007). Meteorological data confirm that July 2009 was a dry month (no effective rainfall) with an average temperature of 27.9º C, whereas December 2006 was humid and relatively cool (average temperature 24.4º C).

Table 6. Comparison of leaf sap osmolality and photosynthetic parameters of mangrove species in the Jobos Bay National Estuarine Research Reserve site obtained during winter (Lugo et al. 2007) and summer seasons (present paper). Temperature and rainfall data are from the Aguirre Station, Salinas, Puerto Rico (http://weather-warehouse.com/).

	Rhizophora	***Laguncularia***	***Avicennia***
SUMMER			
Leaf sap osmolality mmol kg^{-1}	1696	1769	3140
A ($\mu mol\ m^{-2}\ s^{-1}$)	8.4	5.5	5.5
g_s ($mmol\ m^{-2}\ s^{-1}$)	99	53	63
Q leaf ($\mu mol\ m^{-2}\ s^{-1}$)	1242	1177	1253
T leaf (^oC)	38.2	38.6	38.3
WINTER			
Leaf sap osmolality mmol kg^{-1}	1305	988	1799
A ($\mu mol\ m^{-2}\ s^{-1}$)	12.7	10.7	7.9
g_s ($mmol\ m^{-2}\ s^{-1}$)	283	241	185
T leaf (^oC)	29.0	28.0	29.5
	Av T ^oC	Rainfall mm	
July 2009	27.9	0	
December 1986	24.4	52.3	

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EL GUAM-E DEL CULEBRÓN ASECHANDO AL PRESUNTO IMPLICADO

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INTRODUCCIÓN

La isla de Guam en el lejano Océano Pacífico tropical es bastante menor que Puerto Rico pero comparte un sorprendente conjunto de características geográficas. Ubica en lat. 14°N, y 143°E, y consta de 549 km^2 o sea casi un tercio del área de Puerto Rico. Es la mayor y más meridional del archipiélago de las Islas Marianas, colonizadas por España a partir de 1561 como escala de aguada y aprovisionamiento en ruta de los galeones de Acapulco, México a las Islas Filipinas, 2,569 km rumbo al oeste. Guam dista 11,774 km de Méjico. Las islas de paso fueron bautizadas en honor de Mariana de Austria, regente viuda del rey Felipe IV.

Cuando apropiada por el imperio español en 1667 el archipiélago abarcaba unas 16 islitas volcánicas y calizas, la mayoría casi deshabitadas. Guam al sur, la más poblada, tenía unos 50,000 habitantes indígenas de etnia malayo-polinesia denominados con el mote de *chamorros.* De sofisticada cultura prehistórica comparable a la de los Taínos, fueron también rápidamente asimilados a la cultura Católica hispano-mejicana, decimados por enfermedades introducidas y diluidos por el mestizaje. Los gobernadores militares que regentearon a Guam, reprimieron las ansias de independencia de los chamorros, incluyendo una sublevación fallida, que no obstante lograron conservar su idioma e identidad.

La capital, Agaña (Agana en inglés), prosperó con el "situado mejicano" monetario para el desarrollo y mantenimiento del puerto principal de la isla. En contraste a Puerto Rico donde el "situado" fue invertido en la fortificación defensiva de San Juan, el aislamiento remoto de Guam hizo innecesario semejante expendio. El fortín de Santa Águeda sobre un promontorio tierra adentro d el puerto parece ofrecer un abanico de artillería sobre la población civil a sus pies. Se trata apenas de una plataforma rústica de cantos rodados que no compara con el fortín Conde de Mirasol en Vieques, de maciza arquitectura.

En 1898 terminó el dominio de España al perder la Guerra Hispanoamericana. El botín de guerra que recibió Estados Unidos incluyó a Puerto Rico, Filipinas, y su punto de escala, la solitaria isla de Guam. Las restantes Islas Marianas se las vendió España a Alemania al año siguiente dado el afán de Alemania en afianzar su presencia colonial en el Pacífico. Presagio nefasto porque en 1914 el igualmente afanoso Japón entró a la Primera Guerra Mundial contra Alemania y ocupó las Islas Marianas del Norte, anticipando la horrenda confrontación con el coloso de Estados Unidos tras el ataque a Pearl Harbor, Hawaii el 7 de diciembre de 1941.

Horas más tarde los japoneses comenzaron la sangrienta invasión y ocupación de Filipinas que duró hasta 1945. A la vez invadieron a Guam desde las enyuntadas islas principales de las Marianas del Norte, Saipán y Tinian, colonizadas por Japón, con 40%

Figura 1. Ocupación del territorio de Guam por japoneses, 1944.

del área de Guam y distante de esta 200 km. Chamorros asimilados a la colonia japonesa fueron encomendados la administración de Guam. La ocupación de casi tres años de la posesión americana fue tan cruel en el trato de sus habitantes que impidió la unificación de ambos territorios tras las armas americanas recuperar a Guam y conquistar las islas del norte Fig. 1. Medio siglo más tarde Guam reclamaría convertirse en república independiente "asociada" a Estados Unidos. Las Marianas del Norte fueron sometidas en forma cruenta. Murió la soldadesca japonesa de 30,000 y además 20,000 civiles; se ha alegado prefirieron el suicidio a la rendición. Repobla-das con gentes diversas optarían eventualmente por la integración incondicional a la metrópoli y se les concedió el primer "estado libre asociado" americano del Pacífico en 1978. Su población actual, estimada de 80,000 habitantes es la mitad de la de Guam.

A todas luces ambos modelos de organización política como territorios “no incorporados” de Estados Unidos han sido calcados de la experiencia de Puerto Rico. Todas las personas nacidas en las dos unidades del archipiélago son ciudadanos de Estados Unidos con plenos derechos en el continente pero no en sus respectivas patrias, que están sujetas al albedrío congresional. Excluidas de la clausula territorial no cualifican para la estadidad federada. Para mitigar los reclamos de igualdad y autodeterminación cada territorio tiene un delegado en la Cámara de Representantes del Congreso, con participación pero sin voto legislativo, la misma condición que aplica a Puerto Rico e Islas Vírgenes.

Los reclamos de igualdad estatutaria por la población chamorro generó intentos “soberanistas” inaceptables por el Congreso. En la práctica tanto el Congreso como la rama ejecutiva han paliado las desigualdades otorgando participación en programas federales de asistencia social y económica. El Acta Orgánica de Guam en 1950 transfirió la jurisdicción federal de la marina de guerra al Departamento del Interior. Aunque las fuerzas armadas siguieron en control de sus bases, el cambio conllevó la creación de un tribunal de distrito especial y la injerencia de leyes y entidades federales como la Agencia de Protección Ambiental (EPA) y el autónomo Servicio de Pesca y Vida Silvestre (FWS) del Departamento de Agricultura federal (USDA).

La población civil actual de Guam es mitad chamorro; la otra mitad se divide entre filipinos de reciente inmigración y gente de diversas etnias no asimiladas. La población de militares y sus familiares dependientes no se contabiliza ni revela. Ambivalente ante el hecho de su beneficiosa dependencia de la presencia militar estadounidense, los chamorros se refugiaron anímicamente en la veneración de su icónica avifauna nativa compuesta de más de media docena de especies y subespecies endémicas sin contar las dos de murciélagos, bocadillos apetecidos por los criollos.

El caso es similar al de Puerto Rico y su glorificación de la cotorra jíbara (*Amazona vittata*). Por coincidencia las poblaciones remanentes de la cotorra puertorriqueña y la avifauna amenazada de Guam se encuentran en tierras federales sujetas al igual que las privadas a la jurisdicción del Fish and Wildlife Service (por sus siglas en inglés) otorgada por disposición constitucional del *Endangered Species Act* de 1972. En ambos casos dichas aves fueron designadas especies en peligro de extinción amparadas por los poderes prerrogativos federales a través del FWS. La facultad de la agencia de establecer y administrar territorios de hábitat crítico para la pervivencia de las especies elegidas chocaría en el caso de Guam con los intereses propietarios de la milicia y la prioridad de la seguridad nacional. La resolución del conflicto es la trama del siguiente reportaje.

CONTEXTO GEOGRÁFICO DEL PROBLEMA

La importancia militar de Guam ha sido su sitio y situación estratégica como trampolín aéreo y naval para el dominio de la periferia asiática. La guerra contra Japón terminaría en 1945 tras el vuelo de los bombarderos desde Tínian, Marianas del Norte, que descargaron bombas atómicas sobre Hiroshima y Nagasaki. Durante el resto del Siglo 20 Estados Unidos sostuvo desde sus bases en Guam las guerras de Corea y Vietnam, y el detente a China en Taiwán.

La conquista del baluarte Guam con sus excelentes puertos y pistas aéreas costó la vida a más de 18,000 japoneses atrincherados, y oficialmente a casi 8,000 bajas americanas entre muertos y heridos. Al terminar la guerra las fuerzas armadas ampliaron y reconstruyeron sus bases con la expropiación de tierras de nativos sumando casi la tercera parte de la isla. Nos recuerda la toma militar de la mitad de la isla de Vieques con la expulsión de sus propietarios al comienzo de la misma guerra. A despecho de los 68,000 japoneses que murieron aferrados a ambas Marianas, hoy día el 90% del turismo millonario que visita las islas es japonés.

La configuración topográfica de Guam es el de una lengüeta que apunta al norte, de aproximadamente 50 km de largo por unos 15 km de ancho y un cinturón de 7 km por el medio. Con escasa imaginación, desde el espacio tal parece el perfil de un pene en riste con su testículo adosado al sur. La analogía tiene bemoles porque en realidad se trata de geografías físicas y humanas tan distintas como funcionales en ambos extremos.

La base naval aérea Andersen y sus urbanizaciones de apoyo ocupan el municipio de Yigo en la punta nordeste y mitad de la meseta cárstica que define el norte de la isla. La otra mitad cubre el municipio de Dededo que contiene la pista aérea del antiguo *Naval Air Station* (Tiyan) actualmente en manos del gobierno de Guam. El ovoide del sur es montañoso con cimas de 400 metros, suelos volcánicos lateríticos (rojos), y 96 riachos incluyendo las cuencas de cuatro ríos caudalosos. La región está cubierta de bosques y abarca nueve municipios con aldehuelas y una ciudad, Agat, de 5,000 habitantes.

El país suma diecinueve pueblos municipales, la mayoría aldeas de poco más de mil habitantes, incluyendo la capital Agaña. La ciudad principal es Dededo con unos 43,000 habitantes y le sigue Yigo con 20,500. Ambos municipios se dividen el norte de la isla donde ubica la mayor base militar, y proveen la mano de obra civil de la misma.

Aunque la capital (desde 1998 oficialmente “Hagâtña”) solo tiene poco más de 1,000 habitantes en 2.6 km^2, es el eje de una área metropolitana de media docena de pequeñas ciudades que suman 63,000 personas. Con las poblaciones de Dededo y Yigo la mitad norte del país comprende el 82% de la población de Guam. El pueblo principal del sur es Agat, sede de *Apra Harbor*, el puerto comercial y militar más importante, por donde desembarcaron las tropas americanas que reconquistaron a Guam.

El objetivo de la incursión, como había sido de los japoneses invasores, era tomar el baluarte militar del norte. Según mapa disponible, el frente de guerra partió de la acantilada cordillera en la costa oeste del suroeste avanzando hacia el norte en perímetro de costa a costa, dejando a un lado todo el resto de la región sureña y esquivando la capital y su población civil. Desalojar a los japoneses atrincherados en los recovecos cavernosos del carso tomaría casi un mes de lucha cuerpo a cuerpo con la ayuda de lanzallamas, granadas y bombardeo de gas mostaza. El paisaje quedó arrasado. No obstante, en ausencia del estruendo de cañones y explosivos la avifauna de los bosques del sur que no fue escenario de guerra habría evitado impacto directo al ser espantado por el tiroteo del conflicto en su área de alimentación.

La rehabilitación de la meseta devastada acompañó la reconstrucción ampliada del complejo militar existente y de sus espacios circundantes, otrora salpicado de bosques secundarios y dedicados a la ganadería vacuna, carbón vegetal y cultivos como la piña que se dan en pedregales rasos. La disponibilidad de arena de playa y ríos y suelo friable transportado del sur se habrían aprovechado desde que se estableció la armada a principios de siglo. La extensa periferia desnudada por la guerra era más problemática y requirió un ambicioso proyecto de mitigación biogeográfica, la diseminación en volandas de semillas de alguna especie.

Antes de describir la especie escogida viene al punto la experiencia en carne propia del investigador David Quammen (cuyo quehacer se abordará más adelante) quien se vio literalmente 'a gatas' en un remanente desprovisto de de la meseta (traducción del inglés):

"El confín del norte es una meseta porosa de piedra caliza…pero ninguna quebrada la atraviesa y ningún lago puntea la superficie, ya que la caliza absorbe lluvia como una esponja—es decir una esponja petrificada. El suelo es duro, áspero y filoso. El pedregal calizo rasga tus zapatos cuando lo atraviesas. Rebana las rodillas de tus pantalones y las palmas de tus manos, si tienes ocasión de arrastrarte ". (Quammen, 1996 pág. 322).

El testimonio citado es fehaciente de la tribulación padecida por las tropas que lucharon en la meseta. Pero escapó al observador que al interior de la misma existe el acuífero que recoge el agua de lluvia y provee el agua potable para el 82% de la población isleña. A la necesidad de proteger ese recurso se concibió la introducción del árbol *tangan-tangan* (*Leucaena leucocephala*), leguminoso extensamente usado en los trópicos asiáticos para restaurar suelos desgastados por la explotación desmedida.

Tiene capacidad de fijar el nitrógeno que abona su crecimiento a razón de 500 kg/ha por año. Produce 2 mil a 20 mil kg/ha por año de follaje alimenticio para ganado vacuno, cabros y ovejas, aunque resulta tóxico para conejos, caballos, burros, mulas y cerdos. Arbolito de crecimiento rápido e invasivo en tierras yermas y fincas abandonadas. Las bellotas tiernas se consumen como vegetales, las semillas se tuestan como substituto del café. La corteza y raíces se emplean en remedios caseros. Común en la costa sur de Puerto Rico. Nativa de Méjico, se ha naturalizado mundialmente (Little and Wadsworth 1964 págs. 156–157).

La necesidad prioritaria de asegurar el abasto de agua potable para la población civil y militar de Guam fue atendido por la Environmental Protection Agency (por sus siglas en inglés) durante la década de 1970. Al efecto realizó estudios hidrológicos sobre las dimensiones y capacidad de carga del acuífero, limitando el análisis químico a la subyacente influencia salina oceánica. La renuencia de la EPA en abordar problemas de contaminación en deferencia a intereses agro-industriales resultó lesivo a su prestigio científico, según señala la analista Sheila Jasanoff (1990 pág. 123):

"La credibilidad científica le ha sido más difícil a la EPA mantener en su programa de pesticidas que en cualquier otra área de responsabilidad regulatoria. La transferencia del programa a la EPA fue un legado de *Primavera Silenciosa* de Rachel Carson [1961] el libro que no solo inició un nuevo movimiento social, ayudó además a situar los pesticidas en el corazón mismo de la política ambiental". (traducción del inglés).

EL PROBLEMA: UN PAISAJE SILENCIOSO

En 1978 el gobernador de Guam, Ricardo Bordallo, solicitó al FWS que designara como especies en peligro de extinción cuatro aves y dos murciélagos nativos. Un año más tarde el gobernador interino Joseph Ada hizo una segunda petición añadiendo siete especies a la lista. El FWS procedió a la evaluación protocolar de la mayoría de las especies sometidas dejando fuera cuatro. Mientras, el ornitólogo J. Mark Jenkins, adscrito al Departamento de Recursos Naturales y ambientales de Guam (DAWR) realizaba un censo geográfico y estudio ecológico meticuloso de las especies señaladas en 1978-79. Realizado en 1978 y 1979, la publicación de una monografía con sus hallazgos en 1983 provocó una controversia sobre la causa de la disminución y extinción de la avifauna nativa.

Las especies en cuestión habían menguado o desaparecido del paisaje tradicionalmente habitado quedando en silencio el canto de aves. El conjunto estudiado por Jenkins contenía especies que anidaban en los bosques del sur. La mayoría, sin embargo, había cazado insectos y sabandijas en la meseta más o menos descampada del norte y ahora enmalezada con *tangan-tangan* o gramados asperjados con plaguicidas. El estudio de cada ave se acompañó de un mapa de Guam mostrando como se había achicado el área de su avistamiento a través de los años.

Los mapas de todas las especies estudiadas coinciden en mostrar como último refugio de las mismas el 'prepucio' de bosque nativo original al pie del acantilado de 500 pies de la meseta caliza del norte, área conocida como *Ritidian Point.* En su estudio Jenkins clasifica cuatro especies como insectívoras, otras cuatro como omnívoras que consumen insectos y sabandijas además de frutas, flores y vegetación tierna. Solo las dos especies de palomas nativas eran enteramente vegetarianas.

De las ambiguas recomendaciones que presenta su monografía merecen mención las siguientes: 1) que las nueve especies de bosque estudiadas se incorporaran a la lista del Ecological Society of America (por sus siglas en inglés); 2) "que el uso de todos los insecticidas y herbicidas se descontinúen de inmediato…" en las facilidades militares y el barranco de *Ritidian Point*; 3) que se realicen estudios para eliminar dudas sobre la causa de la desaparición de la avifauna de bosque; 4) que se asigne uno o más biólogos federales [FWS] a Guam.

La publicación del estudio de Jenkins con sus recomendaciones en 1983 pasó desapercibido hasta 1984 cuando se publicó en *Nature* un extenso comentario por el prestigioso iconoclasta científico Jared Diamond descartando las teorías que atribuían la extinción de la avifauna a la "-destrucción del hábitat, depredadores introducidos, tormentas y enfermedades." Citando evidencia acopiada por Jenkins implica el uso desmesurado del pesticida DDT por la milicia y también por agricultores especialmente en el sur de la isla. Cuerpos de la golondrinita insectívora *yayahuak* (*Aerodroma vankorensis bartschi*) estudiados por un especialista habían rendido residuos del derivado DDE. El avecilla es notable por anidar en las altas paredes verticales de cuevas oscuras. Encuentra sus niditos por eco-locación como los murciélagos. Los hace de un pegostre de insectos masticados. Colectores arriesgados los despojan para el cotizado mercado de sopa de nido, razón probable por la evaluación de DDT en las aves mismas. Acota Diamond que se continuaba aplicando plaguicidas indiscriminadamente en ausencia de un movimiento ambientalista que se opusiera.

Los biólogos aludidos por propugnar la tesis de la serpiente invasora no tardaron en ripostar en la sección de cartas de *Nature* al año siguiente. Se trata de Christian Grue del notorio *Patuxtent Wildlife Research Center* del FWS, y Julie Savidge, notoria bióloga en la nómina del *División of Aquatic & Wildlife Resources* (DAWR) del gobierno de Guam. Grue cita sus propios análisis de la presencia de DDT y DDE en cuerpos de aves de Guam concluyendo que era "apenas una fracción de niveles letales". Defendió además el continuado uso militar de otros plaguicidas como Malación, organofosfatos y carbomatos "que no persisten en el ambiente".

La bióloga Julie Savidge debe su notoriedad a la fama mediática que le advino por descubrir el verdadero culpable de la avifauna perdida, la serpiente arbórea parda (*Boiga irregularis*) especie exótica invasora. Su carta respuesta a Diamond desestimó el uso de plaguicidas citando a su colega Grue. Descartó además los parásitos, bacterias y virus que el laboratorio del FWS había desestimado, y finalmente descartó a los perros y gatos cimarrones y las ratas como depredadores importantes a favor de su villano elegido.

La culebra nativa de las Islas del Almirantazgo y otras al sur de Guam donde había bases americanas habría llegado a la isla colada en equipo militar temprano en la posguerra. Estaba fichada como presunto implicado por la marina treinta años más tarde cuando la joven Savidge de la *University of Illinois – Urbana* en pos de tema doctoral fue subvencionada para estudiar la serpiente exótica invasora por el FWS y entidades afines, incluyendo seguramente la marina con autorización para recorrer la reserva militar.

El encargo coincidió por un lado con el auge del paradigma invasionista en la bio-ecología anglo-americana, que culpa a las especies foráneas introducidas de maleficios ecológicos como el desplazamiento o depredación de especies endémicas hasta su extinción.

Por otro lado, el Departamento federal de agricultura United States Department of Agriculture (por sus siglas en inglés) y su subsidiaria el FWS se oponían tajantemente a las pretensiones del naciente movimiento ambientalista de proscribir la producción y uso de DDT y plaguicidas análogos en la agricultura y pecuaria. Defendía a las mega-compañías que producían y exportaban plaguicidas, como DuPont, Monsanto y Dow, y las multinacionales agrícolas como Dole que los usaban en otros países.

EL PARAÍSO PERDIDO

Con el sugestivo título (en inglés): "Guam: paraíso perdido para la vida silvestre" la aguzada joven Julie A. Savidge se lanza al abordaje del problema de disminución y extinción de la fauna nativa de Guam, sin limitarse a las aves. Su primicia literaria es un abarcador sumario del descalabro ambiental de la isla y sus consecuencias ecológicas, publicado en el prestigioso "journal" de Inglaterra: *Biological Conservation,* (Savidge 1984).

Adscrita a la agencia ambiental (DAWR) del gobierno territorial y sin vínculo aparente a la milicia, la investigadora hace acopio revelador de observaciones personales, de colegas y fuentes publicadas en su prognosis de la problemática ambiental de Guam. Trasfondo tácito de su pesquisa es el sobregiro de la capacidad de carga humana del territorio isleño, con densidad promedio de 230/km^2. Al efecto, acomete críticamente contra los manejos ambientales de la milicia y de la población nativa.

Comienza con breve reseña histórica del pueblo chamorro en que hace elogio de la cultura antigua de pesca y agricultura suplementada con caza y recolección, y su creencia en *taotaomonas,* los espíritus guardianes de la naturaleza que conminaban a la gente a no destruir la vegetación. Luego entra de lleno al tema dejando entrever su filiación ideológica, la introducción durante el periodo español de especies foráneas de plantas y animales. Destaca el ciervo sambar (*Cervus unicolor*), el cerdo (*Sus scrofa*) y el búfalo de agua (*Bubalus bubalis*), todos asilvestrados en los montes de la isla.

Pasa a considerar los mamíferos nativos que reduce a tres especies de murciélagos. Los de cuevas (*Emballonura semicaudata*) sufrieron las granadas lanzadas en las mismas durante la reconquista. Aquí hace la sorpresiva admisión que siendo especie insectívora habría sido afectada por el uso excesivo de DDT y otros insecticidas por la milicia en la posguerra hasta 1970. Todavía en 1975, afirma, gran parte de Guam era asperjada con cantidades abundantes de Malación para el control de los mosquitos portadores de dengue. Acota que ya el uso de plaguicidas se había limitado a urbanizaciones militares y fincas civiles.

Los *fanihi* ("zorros voladores") murciélagos diurnos, grandes y fruteros, enrarecían por otras razones. El pequeño endémico (*Pteropus tokudae*) se consideraba extinto. La especie mayor (*Pteropus mariannus*) nativa regional de las Islas Marianas había mermado a unos cincuenta en 1978 pero repuntado a ochocientos en 1983 por insumo migratorio de Rota, pequeña isla 48 km al norte de Guam. La verdadera razón por su disminución se atribuye a la tala de sus árboles dormideros y más importantes a la cacería desmedida como bocadillo gourmet tradicional. De poco ha valido la protección por ley. Los cazadores furtivos que usaban redes ahora usan escopetas. De islas con menos restricciones se importaron treinta mil congelados en 1979-'80. En 1981 se prohibió la importación de zorros voladores de todas las Marianas a Guam.

Antes de proseguir con la avifauna es menester comentar sobre cinco especies de ratas que Savidge menciona en su artículo. Se trata de de dos especies de ratas surasiáticas y dos euroasiáticas (Muridae). Contando además el arriero común (*Mus musculus*), todos naturalizados desde tiempos pretéritos. Recién terminada la guerra en 1945 el biólogo Rollin H. Baker fue comisionado por la marina para un estudio ecológico de las tres especies consideradas fauna nativa a respetarse como tal. Inexplicablemente, en su informe hace mención omisa de las dos especies euroasiáticas cosmopolitas, ya que motivaba el estudio la necesidad de proteger los abastos de alimentos almacenados.

Las especies estudiadas fueron la rata de Polinesia (*Rattus exulans*), la rata de Filipinas (*R. mindorensis*), y el ratoncito ya citado. Los hallazgos más notables señalan que las ratas 'nativas' se mantenían en habitáculos específicos, discretos y circunscritos del paisaje natural, alejados de las áreas urbanizadas. Se alimentaban de semillas, insectos, frutas y vegetales. La especie de mayor tamaño, la filipina, trepa árboles y podría depredar nidos de aves, pero la polinesa era más agresiva y no se llevaba con su congénere. Solo el ratoncito se encontraba en todas partes. Las dos ratas cosmopolitas, la de techo (*R. rattus*) y la noruega terrestre (*R. norvegicus*) prefieren las áreas urbanizadas.

El siguiente segmento dedicado a la avifauna es tratado por la bióloga en forma curiosamente salteado y desigual. Se limita a identificar las dos especies de bosque endémicas, el "broadbill" o *chuguanguan* (*Myiagra freicineti*) y el "rail" o *ko-ko* (*Rallus owstoni*). Salta a listar tres especies de humedales afectadas por el drenaje, desmonte y cacería: el pato "mallard" (*Anas oustaleti*), *nganga'* en chamorro, el "rail" de ceja blanca (*Poliolimnas cinereus*), y la reinita "nightingale reed warbler" (*Acrocephalus luscinia*), *ga-karisu*. Menciona al vuelo la drástica disminución del endémico "bridled white-eye" o *nossa* (*Zosterops conspicillata*).

Sigue con un resumen y mapa esquemático que ilustra la reducción geográfica de las aves terrestres de todo el país desde 1950 a la punta norte bajo control de la fuerza aérea y marina en 1983. No menciona para nada el estudio de su colega Mark Jenkins del DAWR realizado en 1978-'79 y publicado el año anterior al artículo de Savidge. Es más, en la nota de agradecimiento a colaboradores hace mención omisa de su compañero agencial. ¿Rivalidad, o enojoso desacuerdo con la postura anti-DDT de Jenkins apoyada por Diamond en el dime y direte del mismo año que publicó su artículo?

Saidge pasa a considerar otras posibilidades para la disminución o desaparición de las aves del bosque. Aunque categoriza todas las especies de comestibles descarta la cacería por estar prohibida en tierras militares. Desecha de plano el impacto del DDT y otros plaguicidas que habían sido usados, admite, extensamente, acogiéndose a la opinión del delegado del FWS Christian Grue, de que eso era cosa del pasado.

La explicación más probable asegura serían las enfermedades o la depredación. Los perros y gatos cimarrones y las ratas son problemáticas en todas la Islas Marianas, pero solo en Guam peligraba la avifauna. El único depredador que no existía en las demás islas era la serpiente arbórea parda (*Boiga irregularis*). Aves y sus huevos constituyen la mayor parte de su dieta y su expansión territorial acompañaba la contracción geográfica de las aves. Savidge había encontrado al presunto implicado para su tesis.

No elimina del todo la posible incidencia de enfermedades como la malaria avícola y otras afines, citando el caso de Hawai y la introducción de sendas especies de mosquitos. Aprovecha para acusar la introducción de aves exóticas como portadores de plagas a poblaciones de aves que nunca habían sido expuestas a las mismas. Pasa por alto que las aves de corral y palomas con sus padecimientos habían sido introducidas desde antaño. Finalmente, se deja ver la costura ideológica al censurar la proliferación del "francolín" negro (*Francolinus francolinus*) pavito-faisán rastrero introducido como especie de caza por el FWS en 1961, y oriundo de la India. Común en todo el sur de Guam, su éxito adaptivo contradice la supuesta voracidad de la serpiente *Boiga.* Establecida en las áreas de sabana y campitos enmalezados frecuentados por las culebras mantenían acopios cazados de 100 a 300 aves por año según el DAWR.

La última parte del artículo redime en parte la intención de exponer el trastorno medio ambiental de Guam. Dedicado a los recursos marinos denuncia el abandono de los métodos y restricciones tradicionales de pesca de subsistencia por la explotación descontrolada de la economía de mercado. Agrava la situación el uso de venenos y explosivos en la pesca de arrecifes. El uso de cloro en lugar de los derivados de plantas (*Barringtonia* y *Derris*) destruye alevines, invertebrados, coral y algas, y es usado igualmente en cursos de agua dulce. La dinamita obtenida ilegalmente destruye corales y peces no recogidos. Por otro lado el turismo crea demanda por recuerdos de coral y conchas. Algunos gastrópodos como el tritón trompeta (*Charonia tritonis*) han enrarecido, siendo el depredador de la estrella de mar "corona de espinas" (*Acanthaster planci*) consumidora de corales constructores de arrecifes. Concluye mencionando de paso la destrucción de la vegetación por cerdos silvestres y fuegos intencionales y accidentales en el sur de la isla promoviendo la invasión de plantas sabaneras como la yerba cortadora "swordgrass" (*Miscanthus floridulus*), dejando cuestas y barrancos desnudos y erosionados.

ASOMA EL ESA Y EL FWS

Respondiendo a las peticiones de 1978-79 del gobierno de Guam, el FWS inicia a finales de 1983 el protocolo de evaluación de la avifauna y "zorros voladores" nativos propuestos para el listado y protección del ESA como especies en peligro de extinción. La distribución geográfica de cada especie recomendada debía ser determinada para ajustarla al criterio estricto de no haber poblaciones de la misma en otras islas. El conjunto legal y reglamentario del ESA otorga al FWS la potestad de hacer valer la protección de especies elegidas estableciendo reservas de "hábitat crítico" administrado por el FWS para preservar y acrecentar el mismo.

Esto resultaría conflictivo con los intereses de la milicia, propietaria de las tierras identificadas como hábitat crítico en Guam. El estudio de Jenkins con sus mapas realizado el año anterior y publicado poco antes de la iniciativa del FWS sería la fuente principal de información para el deslinde del hábitat crítico por el FWS, justo en medio de las tierras militares. La propuesta del FWS fue publicada a finales del 1983, recién publicado el informe de Jenkins al DAWR del año anterior (50 CFR Part 17 FWS) en *Federal Register* Vol. 48, No.230 /11-29-83/ Proposed Rules: 53729.).

El grado de endemicidad de las diez especies y subespecies recomendadas por el DAWR es cuestionable. En primer lugar se da la proclividad de la taxonomía clásica a disgregar poblaciones de aves isleñas de tierra en nuevos taxones según su apariencia, asumiendo su evolución en aislamiento. El juicio tiene más peso en archipiélagos remotos como Guam. Hoy día el análisis comparativo del ADN ha dado al traste con la tradición. También se considera el fenómeno de la metapoblación, en que algunas aves no migratorias ocupan núcleos dispersos en una amplia región, que se subsidian entre sí para subsanar pérdidas o sobrantes de individuos por vaivenes medio ambientales (R.J. Whittaker 1998, *Island Biogeography,* págs. 199-204).

Las siete especies elegidas por el FWS fueron las siguientes: 1) el endémico "Guam broadbill" o *chuguanguang* (*Myiagra freicineti*); 2) la subespecie endémica de martín pescador, "kingfisher" de Micronesia (*Halcyon cinnamomina c.*); 3) la subespecie endémica de "bridled white-eye" o *nossa* (*Zosterops conspicillata c.*); 4) la subespecie endémica de la gallareta común o *pulattat* (*Gallinula chloropus guami*); 5) la subespecie endémica de la golondrinita de cuevas o *yayahuak* , ya citada; 6) la especie endémica "Guam rail" o *ko-ko* (*Rallus owstoni*); 7) la especie endemic de cuervo o *aga* (*Corvus kubaryi*), native además de la islita de Rota donde el FWS encontró en 1982 una población 1,300 en contraste con los 150 a 200 que quedaban en Guam.

Los murciélagos fahini también fueron elegidos por el FWS pero no así las dos especies de tórtola (*Ptilinopus roseicapillus* y *Gallicolumba xxanthonura*) y el cardenal melero (*Myzomela cardenalis saffordi*), *egigi,* por ser comunes en otras islas al norte de Guam.

El caso de la gallinuela ko-ko merece comentario. Fabulada como incapaz de alzar vuelo, alegación desmentida por el estudio bioecológico de la especie por Mark Jenkins quién reveló que el *ko-ko* alzaba vuelos cortos, en efecto como las gallinas domésticas, y acotó que es noctívaga como la culebra *Boiga,* que si es pequeña podría depredar y si adulta atacarla a picotazos para proteger su nido y prole (J.M. Jenkins 1979). Jenkins sugiere su ancestro habría volado desde Las Filipinas por su parecido con la actual especie de allí (*R. philippinensis*). Muy parecido a sus congéneres antillanos *R. elegans* y *R. longirostris* que también saben usar sus alas (H. Raffaele et al. 1998, *A Guide to the Birds of the West Indies*).

En realidad sorprende el parecido de todas las especies del género *Rallus,* que han logrado colonizar desde las Antillas hasta archipiélagos remotos del suroeste del Pacífico pasando por la Mesoamérica continental (J. Diamond 1991, "A new species of rail from the Solomon Islands and convergent evolution of flightlessness", *The Auk,* Vol. 108(3), págs. 461-470). Se consideraba especie de caza hasta 1976 y seguía siéndolo furtivamente. También era víctima de gatos realengos, lagartos monitores grandes y atropellada por automóviles. Su dieta omnívora de moluscos, insectos, lagartijas y hasta carroña lo exponía a la bioacumulación maligna de plaguicidas. Su selección para el ESA fue adelantada de emergencia en abril de 1984, y posteriormente se recogieron algunos para reproducción en cautiverio por zoológicos especializados en Estados Unidos.

Lo mismo se haría con el "broadbill" o *chuguanguang*, ave decididamente endémico por su adaptación evolutiva de pitirre virtual (“flycatcher”) con aspiración de convertirse en pájaro carpintero según descrito por Jenkins. Ave agresivamente territorial, dispuesto a proteger a picotazos su nido de ratas y culebras trepadoras, pero sentenciado por su dieta de insectos a la maldición de los plaguicidas. Su crianza en cautiverio se ha logrado en el continente.

La propuesta del FWS especula sobre posibles causas de la disminución de la avifauna mencionando la incidencia de enfermedades citando el caso de Hawaii. Descarta la sobre-explotación para cualquier propósito, sorprendente aseveración habiendo reconocido la cacería del *ko-ko* y el saqueo de nidos de la golondrinita *yayahuak*. A despecho de la imputación de Jenkins concluye que el posible impacto de plaguicidas era cosa del pasado pasando por alto la persistencia de los mismos. Finalmente acoge la depredación como causa probable y describe a los presuntos sospechosos. Menciona de paso gatos, perros y ratas, y el lagarto monitor “de mangle” (*Varanus indicus*) que no trepa árboles. Especie nativa del norte de Australia, Nueva Guinea e islas menores de la región donde habría sido introducido en la prehistoria por navegantes polinesios que los llevaban como alimento proteico portátil. De porte mediano (tres a cuatro pies los mayores, la mitad rabo). Carnívoro playero que nada para pescar al igual que internarse tierra adentro para atracar gallineros y rebuscar en los basureros. El monitor no habría distinguido entre una gallinita común y una gallinuela *ko-ko* que encontrase en el camino. Introducido en Guam por los japoneses para controlar las ratas.

En la posguerra avicultores chamorros le piden a los americanos controlarlos. Se introduce al efecto el sapo tóxico *Bufo marinus* que los disminuyo, proliferando las ratas. Otros protestaron porque el lagarto es comestible y apetecido por muchos.

A fin de cuentas la propuesta del FWS oficializa la designación del presunto implicado, la serpiente arbórea parda (*Boiga irregularis*), también conocida como la “serpiente ratera de Filipinas”. El emplazamiento admite que el impacto de los depredadores exóticos era desconocido. El pliego concluye con la salvedad de que la determinación de “Critical Habitat” no era “prudente ni determinable” en aquel momento. El entrelineas sugiere que había que negociar con las fuerzas armadas.

A fin de cuentas la propuesta del FWS oficializa la identificación del presunto implicado, la serpiente arbórea parda (*Boiga irregularis*) también conocida como “serpiente ratera de Filipinas”. El emplazamiento admite que el impacto de los depredadores exóticos era desconocido. El pliego concluye con la salvedad de que la determinación de “Critical Habitat” no era prudente ni determinable “en aquel momento”. El entrelíneas sugiere que había que negociar con los poderes militares.

MASACRE IMPUTADA: LA TESIS DEL CULEBRÓN

En 1987, la bióloga Savidge publica un *précis* de su tesis doctoral titulada (en inglés) “Extinción de una avifauna isleña de bosque por una serpiente introducida” (J.A. Savidge 1987 *Ecology* 68 (3), págs. 660–668). Metódicamente redactada, pretende apuntalar con evidencia experimental, encuestas, observaciones personales, testimoniales y referencias pertinentes la hipótesis acusatoria adelantada cuatro años antes contra la serpiente exótica invasiva *Boiga irregularis.*

Su exposición postula demostrar correlación circunstancial entre la presencia y expansión geográfica de la serpiente, sus atributos fisiológicos, hábitos y dieta con la disminución y extinción del conjunto de aves de Guam reconocidas por el FWS como en peligro de extinción. Reclama primicia del primer caso de una culebra culpable por la extinción de otras especies.

De salida descarta otras posibles causas comenzando con la contaminación por plaguicidas postulado por su contrario Mark Jenkins. De nuevo cita la opinión de encargo del agente de Patuxent FWS Christan Grue, cuyo estudio de 1981 había encontrado residuos mínimos de DDT en lagartijos esquincos y musarañas (*Suncus*) en nivel menor que el requerido para afectar aves y mamíferos pequeños (dejando entrever que a mayor tamaño y más larga vida sí habría impacto). En su riposta a Diamond, Grue había concluido, según repite Savidge, que "ni el pasado ni el presente uso de plaguicidas en Guam parece responsable por el continuado declive de la población de aves nativas de la isla". Ignora la bioacumulación en aves insectívoras, menos obvio en animalejos de corta vida.

Savidge despacha someramente la cacería, la competencia con aves introducidas, la modificación del hábitat, enfermedades exóticas y depredación por varios vertebrados introducidos. Sobre la cacería afirma que "la mayoría" de las aves de bosque ha tenido "protección legal" y estaba prohibida en tierras militares, aunque la caza furtiva podría haberle causado "stress" a ciertas poblaciones.

De paso reconoce que durante la guerra "grandes áreas de vegetación fueron arrasadas y algún hábitat destruido" y posteriormente invadido por malezas de *tangantangan* o mesquite (*Leucaena leucocephala*). No obstante, asegura que suficiente hábitat nativo persistía al norte y sur de Guam para sostener poblaciones "saludables" de aves. No hace mención de la devastación forestal y urbana causado por el súper-tifón Pamela en 1976 con vientos de 240 km/hora. ¿Cuántas aves amenazadas habrá barrido de la isla?

Las últimas causas posibles a ser descartadas por la bióloga le resultaron más problemáticas. Confía en estudios del FWS de la incidencia de bacterias, virus y parásitos en aves nativas y de corral (excluyendo la contaminación por plaguicidas) para concluir que no había evidencia de semejantes infecciones en las aves de bosque de Guam.

Según ella la depredación por perros, gatos, monitores y tres especies de ratas existe en otras islas Marianas, pero en Guam afirma que escasean los realengos y también las ratas, implicados todos en extinciones de aves en otras islas. Equivocadamente afirma que los lagartos monitores llevaban siglos en Guam y que estudios de contenido estomacal en áreas de abundancia de aves indicaban un consumo de solo 4% de aves y sus huevos. Solamente la serpiente *Boiga* quedaba como depredador arbóreo y terrestre de hábitos nocturnos y reconocido depredador de nidos de aves. Concluye que el resto de su trabajo lo dedica a evaluar la "hipótesis" de culpabilidad (ya adjudicada) de *Boiga* por el declive de la avifauna de Guam por su depredación de huevos, crías y adultos de las aves. Inexplicablemente pasa por alto la posible depredación de aves al vuelo por aves de rapiña.

DESFILE DE PRUEBAS

Propone evaluar tres predicciones: 1) que la distribución espacial (geográfica) y temporal (cronológica) de *Boiga* se correlaciona con la contracción territorial de la avifauna; 2) que la tasa de depredación debía ser mayor donde las aves han disminuido que donde su población es estable; 3) que las presas alternativas de la serpiente hayan disminuido en patrón similar a las aves.

Para la primera predicción utiliza records documentales históricos y un cuestionario.

Artículos de periódico y datos recopilados por el DAWR se compaginaron con los hallazgos de un cuestionario sometido a muestras de población chamorro en el norte, centro y sur de Guam, asociados a la agricultura y granjas avícolas. Los resultados fueron ilustrados en un mapa que muestra la presencia y expansión territorial de la serpiente invasora según la fecha del dato.

Predeciblemente la invasión de la serpiente *Boiga* fue detectado por primera vez a comienzo de la década de 1950 en la región sur-central de Guam y se presume habría desembarcado escondido en equipo militar por el puerto principal en Agat desde 1945. Se estima que se extendió primero por el óvalo semi-boscoso del sur a razón de 1.6 km por año. Las observaciones sobre su presencia se multiplican a partir de 1963 indicando una expansión inicial hacia el sur y desde 1965 hacia la meseta cársica norteña. Arriba a las tierras militares del norte en 1977 catorce años más tarde.

Al año siguiente se registran 15 apagones por corto-circuitos atribuidos a la culebra cuando escala tirantes de postes de alta tensión que a falta de árboles ocupan la explanada militar. Los apagones aumentarían a 23 en 1979, 31 en 1980, 67 en 1981 y 82 1982. En este año la serpiente habría llegado a la punta norte de la isla y a cuatro años de empezar los apagones se detienen los mismos poniendo conos contra culebras en los tirantes de los postes. Hasta entonces no parece haber tenido gran prioridad resolver el problema ni controlar la serpiente.

La supuesta correlación de la expansión de *Boiga* con la disminución de las aves comienza con una "comunicación personal" no documentada del DAWR que alega cuatro especies pequeñas de aves habían desaparecido del bosque central del sur en las inmediaciones del Naval Magazine (NM), depósito de municiones aislado en medio de un amplio bosque restricto. Al comienzo de la década de 1970 casi todas las aves nativas se observaban en la mitad norte de la isla coincidente con la presencia de la serpiente en el resto del país. La pretendida correlación resulta espuria al considerar que las aves cazaban insectos en el norte pero pernoctaban y anidaban en el sur. La serpiente se habría alimentado más de ratas y sabandijas que de aves durante los diez años hasta 1981 que las aves todavía frecuentaban las malezas de la punta noroeste, habiendo desaparecido de las urbanizaciones militares cuyos extensos gramados y campos deportivos se asperjaban con plaguicidas.

La segunda predicción propone demostrar la capacidad de *Boiga* para la depredación nocturna cuando las aves se acogen a sus nidos. Al efecto la bióloga establece transectos de trampas de embudo a través de sectores con variados remanentes de aves. Usa de carnada pequeñas codornices (*Coturnix*) criados en Guam por sus huevos y carne como bocadillos gourmet, en lugar de pedestres pollos domésticos. No está claro qué raza de codorniz doméstica se utilizó. *C. chinensis* y *C. japonica son* de antigua crianza en los países orientales. Bocadillo adecuado también para serpientes adultas de tamaño promedio, tres a seis pies de largo. En el bosque cuelga las trampas de ramas a distancia sobre el suelo, evitando sin decirlo que les entraran ratas. En las áreas descampadas las coloca en el suelo presumiendo que a falta de árboles las aves anidarían en el suelo!

Las trampas se colocaron a intervalos de 160 metros lineales en siete ambientes distintos y dejados de día y noche (con agua y alpiste para los señuelos) excepto en la franja costera de Ritidian donde los monitores "perturbaron" 18 de 21 trampas de ensayo obligando a colocarlas solo de noche. Las trampas eran visitadas diariamente o cada dos días, y eliminada al consumirse la carnada. La gráfica comparativa de todos los transectos muestra curvas cumulativas durante catorce días.

Los resultados están plagados de contradicciones y manipulación estadigráfica. La mayor incidencia aparente de depredación por *Boiga* ocurre en áreas del norte donde ya no se veía avifauna nativa en los amplios bosques militares restringidos del Naval Communications Center (NCS) y el "northwest forest" (NWF). El NWF con 15 km^2 junto al NCS con 5.3 km^2 suman 20.3 km^2 de área boscosa bajo dominio militar. Más la base Andersen de la fuerza aérea con 9.8 km^2 suma casi 30 km^2 de propiedad militar en la punta norte de Guam. Las 28 hectáreas de bosque del Naval Magazine en el corazón del sur presentaba un cuadro similar. Setenta y cinco porciento de las avecillas carnadas fueron devorados por serpientes dentro de cuatro (NCS) a nueve noches (NM) y NWF, "excluyendo depredación por monitores y ratas". A excepción del descampado de la NASA donde la depredación por ratas fue de 87%. El calce de la gráfica recalca: "Depredación por ratas y lagartos monitores fue excluido del análisis". Evidentemente la intención de la bióloga es escamotear el impacto de las ratas y monitores.

Savidge concluye el análisis de su Predicción número 2 preguntándose el porqué de la mayor depredación de codornices por monitores y menor por *Boiga* en Ritidian que en otras localidades. Sospecha que la serpiente estaba impactando al reptil, habiéndose encontrado huevos del lagarto en estómagos de serpientes. Tratándose de una franja estrecha de costa bordeada de acantilado los lagartos estaban en su hábitat y a las recién llegadas serpientes tendrían que conformarse con 38% de la cosecha de huevos de codornices. De todos modos según afirma contradiciendo sus propios datos: "las aves [nativas] habían sido virtualmente eliminadas del área", el último refugio documentado de toda la avifauna del bosque.

La tercera predicción es que los animalitos presas alternativas de *Boiga* habrían disminuido en un patrón similar al de las aves. Compara densidades de pequeños mamíferos publicados en 1946 y 1974, antes de la invasión de la serpiente en varios lugares con las capturas obtenidas por ella en 1984-'85 en los mismos lugares con métodos similares a los estudios anteriores.

Obtuvo resultados de contraste entre dos tipos de hábitat. En los "fields" de pastizales regados de matojos y rodeados de boscaje le sorprendió un declive de 94%, de 42.5 a 2.8 mamíferos por hectárea, solo ratas y ratones y abundantes serpientes. En la "savanna" descampada, sin embargo, encontró pocas serpientes pero abundancia de musarañas (*Suncus murinus*) la especie más común en 1974 pero ausente en los "fields" que investigó. Atribuye las escasez de serpientes a la falta de escondrijos por el predominio de penachos enjutos de yerba cortadora "swordgrass" (*Miscanthus floridulus*). Las musarañas evidentemente encontraban refugio entre sus raíces. Otro estudio por el inefable Christian Grue en 1986 concluyó que la abundancia y distribución de musarañas colectadas para un estudio de plaguicidas era similar al de las aves nativas a excepción de áreas urbanizadas, apoyando la predicción del declive de presas alternativas de *Boiga* cónsono con el de aves.

La bióloga remacha su tercera predicción con el ensayo de nidos artificiales con huevos de codorniz en el bosque del norte. Antes de que llegara la serpiente 31% de 51 nidos fueron depredados por ratas pero dos años más tarde tras colonización por *Boiga* un total de 30 nidos (100%) fueron decimados. Añade en paréntesis: "(37% de 30 nidos)". La ambigüedad se impone. ¿Cuánto por serpientes y cuanto por ratas? Tampoco consideró la depredación por cerdos salvajes (*babuen machalek*) que en 1984 sumaban 110 / km^2 en dicho bosque.

Savidge concluye su exposición doctoral con una discusión de los hallazgos culpatorios de *Boiga.* La mayoría de las serpientes capturadas medían más o menos un pies (120 cm), por tanto pequeñas. Argumenta que depredarían las aves pequeñas como las *nossa* (*Zosterops*), especie gregaria que dormía en fila susceptible a ser consumidas una tras otra, hasta tres por noche según su propia observación anecdótica de aves enjauladas, difícil de tragar. Las culebritas incapaces de engullir adultos de las restantes especies mayores depredarían sus huevos y crías con impunidad. Las *nossas* se vieron por última vez en 1983.

Para 1983 las serpientes llevaban veinte años poblando el bosque donde anidaban las *nossas.* Debían sobrar las culebras adultas. ¿Por qué se capturaban mayormente pequeñas? Se le escapa a la bióloga que donde escaseaba *Boiga* abundaban las musarañas, agresivas devoradoras de serpientes adultas, descomunal voracidad para su diminuto tamaño. Por otro lado la tesis presenta un listado de las especies "residentes" de aves, omitiendo mención de las migratorias incluyendo las de rapiña, que incluye dos especies de halconcito del género *Accipiter* cuyas presas raptadas al vuelo se limitan al tamaño de las *nossas.*

La discusión reconoce que las aves nativas de mayor tamaño como el cuervo *aga* y la gallinuela *ko-ko* fueron las últimas especies en disminuir en varias áreas. El martín pescador (*Halcyon*) también de las mayores, anida en inexpugnables huecos estrechos de árboles, gran pico en riste. Se le escapa mencionar el igualmente corpulento y defensivo "broadbill" *chuguanguang* con dotes de pájaro carpintero armado de un pico formidable. Otra especie que se excluye de depredación por la serpiente es la golondrinita de cuevas *yayahuak.* Las paredes lisas de las cuevas impedían a las serpientes escalarlas hasta los nidos.

A final de cuentas Savidge intenta explicar la persistencia de *Boiga* a pesar de la desaparición de su presa principal la avifauna de bosque. Calcula alta la densidad de 16 serpientes por hectárea pero acepta una densidad documentada para Nueva Guinea de 69 aves por hectárea. Con poca aves en Guam la serpiente opta por presas alternativas para mantener un alto nivel de población. Encuentra que las serpientes jóvenes consumen lagartijos esquincos y geckos con aparente capacidad reproductiva para resistir la depredación.

El artículo que hace síntesis de la tesis concluye con especulación teórica sobre la habilidad de las serpientes para percibir sus presas de noche. A todas luces la bióloga no se molestó en estudiar la biología del género *Boiga,* unas cincuenta especies conocidas como serpientes "ojos de gato" por sus pupilas verticales que les permite como a los gatos ver de noche al concentrar tenues reflejos nocturnos. Además, algunas serpientes perciben la radiación calorífica de sus presas.

Cierra el opúsculo sin considerar medidas para combatir la serpiente invasora ni proponer refugios para la avifauna amenazada. El precedente de control biológico ensayado con la introducción del sapo tóxico contra los monitores no se le ocurriría a la milicia, ni al FWS, ni al DAWR. Se sabe que el sapo *Bufo marinus* es capaz de atosigar con su veneno a las culebras que intentan engullirlo, especialmente las ajenas a la patria americana del sapo como *B oiga.* Quién sabe si el sapo llegó a Guam desde Puerto Rico, que en 1935 exportó la especie al trópico cañero de Australia para acabar con la plaga de caculos (*Diaprepes*) y acabó haciendo escantes con los ingenuos carnívoros del país incluyendo la serpiente nativa *Boiga*. Introducida a Guam para decimar a los monitores. ¿Habría el sapo tóxico *kairo* contribuido a disminuir las serpientes? En un artículo posterior sobre la dieta de la serpiente (Savidge 1988), la bióloga informa hallazgos separados de tres serpientes muertas al atosigarse sapos tóxicos.

Tampoco se aprovecharía la iniciativa de Hawai para el control de ratas. Allá se introdujo el búho *Tyto alba* en 1958 y de nuevo en 1963, capaz de depredar culebras además de ratas. Hay otras especies de búho (como el múcaro *Otus nudipes* de Puerto Rico) más adaptados a las condiciones de Guam. El desinterés oficial por controlar la población de *Boiga* levanta sospecha de mantener la serpiente como chivo expiatorio para desviar la culpabilidad de la armada por la eliminación de la avifauna a consecuencia del uso desmedido y constante de plaguicidas.

Aprobada su tesis en 1986 Savidge obtuvo su doctorado. Merced a la difusión mediática patrocinada indudablemente por las autoridades, se torna causa célebre ejemplar el caso de *Boiga* entre biólogos del paradigma invasionista. Prolifera la publicación de artículos como el de J. Carey (1987 "Massacre on Guam" *National Wildlife,* Vol. 26 (5) págs. 13–15). A la misma vez sale el de S. Pimm (1987 "The snake that ate Guam" *Trends in Ecology and Evolution"* Vol. 2 (10)). Ambos se publican el mismo año que la síntesis doctoral de Savidge, diríase que pisándole los talones. La publicidad le valió a la bióloga obtener empleo un año después en el departamento de dasonomía, pesquería y vida silvestre de la Universidad de Nebraska, destinó un tanto distante de Guam. Sería el comienzo de una carrera exitosa. En el 2004 asciende a catedrática de estudios graduados en la Universidad de Colorado donde había iniciado sus estudios de biología. Irónicamente, se destacaría como especialista del búho excavador de las praderas (*Athene cunicularia*), habiendo pasado por alto el potencial de los búhos en el control nocturno de ratas y culebras en Guam.

POSDATAS A POSTERIORI

Al año de publicarse la síntesis de su tesis, la bióloga publica el primero de dos artículos en que trata temas de su investigación doctoral no incluidos en la versión abreviada. Quizás atendiendo reclamos de lectores aparece: J.A. Savidge (1988 "Food habits of Boiga irregularis, an introduced predator on Guam". *Journal of Herpetology* Vol. 22 (3) págs. 275 – 282). Cuatro años más tarde, dando largas a sus hallazgos inéditos produce: J.A. Savidge, et al. (1992 "Was disease involved in the decimation of Guam's avifauna?" *Journal of Wildlife Disease* Vol. 28 (2) págs. 206–214). Las revelaciones de ambos artículos merecen comentario.

El estudio de la dieta de la serpiente se realizó con necropsias de culebras muertas recogidas entre 1982 y 1986 más datos de 1967 a 1981 suplidos por el DAWR. Del total de 683 especímenes examinados (89% por DAWR), 353, casi la mitad (52%) contenían presas. Los resultados sorprenden. La tabulación de los mismos y su interpretación indican que solo el 28.1% de las presas eran de aves y sus huevos. Se explica que: "La mayoría de las aves y sus huevos eran de gallinas domésticas o asilvestradas debido a la casi ausencia de aves nativas de bosque en Guam".

Las escasas excepciones son reveladoras. Algunas aves nativas de buen tamaño atosigaron serpientes matándolas o siendo vomitadas a medio digerir. Se listan dos martín pescador (*Halcyon*), una tórtola frutera (*Ptilinopus*), un cardenal melero (*Myzomela*), un drongo negro exótico (*Dicrurus macrocercus*), y solo una gallinuela *ko-ko.* Hubo dos casos de serpientes hueveras. Cada uno con dos huevos, de gallina silvestre y de tórtola filipina exótica (*Streptoltelia bitorguata*). Las presas principales de las 160 culebras de áreas de bosque aisladas donde apenas había aves consistían en 93% de los especímenes de lagartijos diversos y sus huevos. En 7.2% habían ratas (4%) y musarañas (3.2%) tabulado como porciento del total de 353 especímenes estudiados. Casos excepcionales incluyen las tres serpientes muertas por engullir el sapo tóxico *Bufo marinus* y un caso de costilla asada ("sparerib") tomado de una barbacoa.

El segundo artículo de Savidge (1992) con resultados inéditos de su tesis presenta hallazgos tan sorprendentes como el de su primera posdata. Al descartar las enfermedades como causal de la extinción de la avifauna deja ver tanto su inclinación ideológica como causas de mortalidad avícola que no involucran a la serpiente invasora. Comienza remachando con los juicios consabidos la exclusión del uso y abuso de plaguicidas como posible causa. A la vez descarta la introducción de aves exóticas como portadores de enfermedades, e identifica siete especies naturalizadas cuya sangre fue analizada para la presencia de patógenos y el conjunto eximido de posible transmisión de males a la avifauna amenazada.

Las aves exóticas cuya sangre fue analizada incluía especies migratorias y domésticas: pollos, codornices, patos, palomas y cotorras. También se obtuvo sangre de aves nativas capturadas y luego soltadas ilesas. Todos los análisis resultaron negativos. Sin embargo, un hallazgo insospechado dejo ver otras causas de mortalidad de aves nativas. Los cadáveres de trece especímenes recogidos indicaron muertes traumáticas al chocar con automóviles y aviones, y ataque inconclusas de serpientes. Ochenta y cinco cuerpos de especies no amenazadas murieron por las mismas causas, 40% al ser impactados por vehículos, perros o cazadores. Trece aves de bosque en cautiverio fallecieron por accidentes o trato inepto. En resumen, la sobrepoblación humana de Guam había eliminado muchas más aves que la serpiente *Boiga.*

ACOTA UN PATRIOTA

La conciencia nacional del pueblo chamorro de Guam es un legado de la colonización española. Con el propósito de domeñar a los anómicos y rebeldes nativos los gobernadores militares impusieron la hispanización reubicando el campesinado disperso de la ruralía a pequeñas aldeas con administración pública municipal subordinada al gobierno colonial de la capital en el puerto de Agana. La conversión al catolicismo se le encomendó al jesuita Diego de San Vitores, asesinado por un cacique nativo en 1672 desatando una guerra de veinticinco años entre conversos y anti-españoles. Tras la pacificación los sacerdotes españoles llegaron a fungir como regentes virtuales de la vida comunitaria, hermanando la población chamorra con países independientes de la misma fé. En la educación parece haber prevalecido el modelo jesuita de respetar el idioma indígena como se hizo en Paraguay con el idioma Guaraní, traduciendo las Escrituras al chamorro, asegurando así la pervivencia de ese idioma (Lanny Thompson 2010 "Guam: The ship metaphor and military rule" págs. 227–245 en *Imperial Archipelago.* Honolulu: University of Hawaii Press).

En 1995 el delegado de Guam al Congreso, partícipe con voz pero sin voto pero sin voto como el comisionado residente de Puerto Rico, depuso ante el comité de recursos de la Cámara en protesta por el Refugio de Vida Silvestre de Guam establecido por el FWS en 1994. El honorable Robert A. Underwood manifestó que el refugio y su opción adicional ("overlay") sobre tierras militares no aportaban a la protección de especies amenazadas. El problema insistió no se debía a la pérdida de hábitat sino que ya había sido adjudicado a la depredación por la serpiente invasora *Boiga.*

Cercar un refugio, argumentó, no impediría la entrada de la serpiente ni que atacara aves, pero mantendría fuera "nuestra gente".

Mejor sería dedicar los recursos a combatir la serpiente. Acusa al FWS de chantajear al gobierno de Guam que de oponerse a la cesión de una propiedad militar para un refugio simple, se expondría al criterio de "hábitat crítico" dispuesto por el ESA implicando control omnímodo sobre tierras militares. Underwood reclama un procedimiento para des-establecer el refugio ya establecido y culpa a grupos ambientalistas del exterior por influenciar la política del FWS.

¿Para quién trabajaba Underwood? Delegado por Guam al Congreso desde 1993 hasta el 2003. Chamorro de nacimiento (1948), educador formado en universidades de California y profesor en la Universidad de Guam. Aspirante delegado demócrata favorecido por la derrota del Republicano H.W. Bush por el demócrata Clinton para presidente de Estados Unidos. Propulsor soberanista de los derechos chamorros somete de entrada a la Cámara de Representantes su primera pieza legislativa, el "Guam Commonwealth Act" para establecer gobierno autónomo, la preservación de la cultura chamorro (reprimida en pos de la asimilación), y "consentimiento mutuo" sobre políticas federales aplicables a Guam. El proyecto de ley no llegó al pleno y sería rechazado en las ocasiones sucesivas que lo presentó.

El refugio objetado por Underwood es el "Guam National Wildlife Refuge", en la franja de costa de Ritidian Point, al pié del acantilado de la meseta cársica del norte de la isla. El área de 1,203 acres (832 acres de tierra y 371 acres de arrecifes y bajamar) fue donado por la marina al FWS en 1993 sin ataduras para evitar la cesión de derechos sobre otras siete áreas de hábitat crítico designadas como "military overlay" sumando 22,456 acres en que la milicia no permitiría la entrada de civiles, aunque tomaría en cuenta la opinión del FWS en su manejo. El parque de Ritidian se ha convertido en una atracción turística que recibe 90 mil visitantes al año.

La pataleta de Underwood resultó en la aprobación en 1994 de su proyecto de ley para la devolución de tierras incautadas por las fuerzas armadas tras la guerra que ya no eran esenciales para la defensa nacional. Más de 3,000 acres fueron transferidas para parques, escuelas y viviendas de interés social. Posteriormente, en el año 2000 logra legislación que otorgaba a Guam primera opción en la adquisición de tierras militares excedentes. Previamente las agencias federales tenían prioridad.

No obstante, la objeción del Delegado al refugio del FWS obedecía a su participación en el Comité de los Servicios Armados de la Cámara, donde cultivó relaciones de reciprocidad con la milicia. Así pudo recabar la búsqueda de bombas sin detonar de gas mostaza lanzadas durante la invasión americana. Underwood se retiró del Congreso en el año 2003. Había servido además en los comités de educación y trabajo, seguridad nacional y recursos naturales. Posteriormente propulsa el reconocimiento del idioma chamorro y su enseñanza en las escuelas, aceptado por ley en el 2013. Regresa a la Universidad de Guam como presidente de la misma en el año 2008.

OTROS TESTIMONIOS: ¿Y TU *BOIGA*, DONDE ESTÁ?

A final de cuentas la tesis de Savidge no pasó de ser una conjetura acusatoria conveniente para desactivar y desviar la confrontación entre el poderío militar y el FWS. Por otro lado se ofrecen dos testimonios ajenos a la polémica, sobre la presencia de la serpiente *Boiga* en el escenario de Guam.

El primer caso es el del soldado japonés, sargento Shoichi Yokoi, descubierto en un boscaje ralo del sur de Guam en 1972, a casi 28 años de terminada la guerra. Tenía 57 años de edad y estaba saludable gracias a la dieta que había llevado desde quedar aislado al interior despoblado de la cuenca del río Talofolo (el más caudaloso de la isla) separado del frente de guerra que avanzaba hacia el norte. Entrevistas posteriores a su encontronazo y captura por jóvenes pescadores chamorros dieron a conocer los talentos personales que le permitieron sobrevivir escondido tanto tiempo. Costurero de joven pudo proveerse un ajuar con géneros textiles obtenidos de la vegetación y las tijeras de campaña con que se recortaba el cabello y barba. Construyó una guarida cómoda debajo de una cepa de bambúes y hasta un retrete sobre el cauce de una quebrada subterránea. Su aposento se conserva reconstruido tras un tifón como una procurada atracción turística. Llevó una dieta balanceada de frutas y vegetales como cocos, panas, mangos y guayabas con fuentes proteicas necesarias. Pescó anguilas, camarones y cangrejos y recoge moluscos. Su bocado preferido eran las ratas (favoritas de las cocinas orientales). Logra cazar un cerdo con el que se intoxicó y nunca más. Habrá aprovechado algunas gallinitas cimarronas y sus huevos.

Pero no se ha constado que haya cazado serpiente alguna, bocado gourmet en Japón como en otros países del sureste de Asia. Según la cartografía de Savidge, para 1968 la serpiente *Boiga* había poblado todo el sur de Guam. Resulta difícil creer que en los seis años siguientes el fugitivo japonés no se haya topado con alguna en los nidos de ratas donde la culebra se escondía de día y también las cazaba.

El segundo testimonio aparece insertado en un tratado enciclopédico populachero que pretende introducir al público lego a la biogeografía. Se trata de David Quammen (1996 *The Song of the Dodo, Island biogeography in an age of extinctions,* New York, Scribner). Escritor de estilo coloquial, novelesco y periodístico. Gusta de investigar con entrevistas y observación directa. Autodidacta evidente, muestra apego inusitado a la vida y obra del naturalista Alfred Russell Wallace y su formulación independiente de la teoría de evolución natural y distribución geográfica de las especies, publicada en 1858 conjuntamente con el trabajo coincidente de Charles Darwin.

Quammen le dedica el primer y más extenso capítulo de su libro a Wallace, contrastando su figura de humilde autodidacta que se sustentaba colectando especies exóticas en lejanas tierras para museos con la vida regalada del aburguesado Darwin. Narra por extenso el chisme de cómo Darwin al enterarse de la primicia de Wallace abusa de la confianza y deferencia que le guardaba el joven para retener el manuscrito enviadole hasta completar con viso de plagio el suyo y presentar ambos trabajos conjuntamente. Se le escapa a Quammen que ambos teóricos debieron su iluminación crítica al ensayo sobre población de Thomas Malthus, publicado cuarenta años antes.

Habiendo leído la literatura sensacionalista sobre *Boiga,* Quammen tramita una visita a Guam para ver el caso con sus propios ojos. Aterriza al final de los años ’80 (no dice cuando) y se le asigna de cicerone al biólogo oficial de la armada Thomas Fritts con su ayudante Gordon Rodda, ambos herpetólogos que le darían acceso a los espacios vedados de las bases militares. Lo llevarían en excursiones para capturar serpientes y serían su fuente principal de información y desinformación sobre las mismas.

El reportaje más objetivo del escritor sería su descripción del paisaje topográfico (ya citado) y urbanizado de la base recorrida. Describe someramente “un pequeño mundo hermético” de patios gramados y campos de golf, todo cercado de “cyclone” bordeado de matorrales. Adentro, “un terreno banal de segadoras, rastrillos y la guerra interminable contra el “crabgrass” (no menciona el uso de herbicidas).

Al salir de su motel al amanezca de haber llegado encuentra sobre el pavimento de entrada su primera serpiente, muerta, augurio que lo deja perplejo. ¿Qué podría significar semejante presente? La noche anterior lo había recibido en el aero-puerto el simpático Rodda quién a la noche siguiente lo lleva de excursión a capturar serpientes por el perímetro cercado de la base en camioneta. Al divisar una le echa mano y deposita en un saco que amarra y carga en el vehículo rumbo al laboratorio. Antes de regresar a su habitación se habían recogido catorce.

En amena conversación el guía aprovecha para relatar los horrores fabulados de la serpiente. ¡Más de quinientos apagones costando millones de dólares! ¡La decisión de la Autoridad de Energía Eléctrica de cortar el servicio de noche! Savidge documentó 218 apagones en cuatro años hasta 1982 cuando se puso fin al problema colocando conos anti-culebra en los tirantes de los postes. ¡El temible ataque a los testículos colgantes por serpientes que penetran por los desagües de los retretes! ¡El robo de hamburguesas de las barbacoas! ¿Cuál sería la densidad de serpientes? A la pregunta de Quammen Rodda estima que trece mil por milla cuadrada. Asoma la sospecha; semejante número de culebras requería mucho alimento. Con sorna el escritor comenta que los miles, quizás millones de culebras que habría en Guam mal se recogían cogiendo a mano el puñado de aquella noche.

¿Habrá caído el escritor en celada urdida por un duo dinámico de científicos mercenarios al servicio de la armada? ¿Se habría vaciado la colección de especímenes del laboratorio para sembrar el ‘show’ de la verja?

Según Quammen, gran parte de las dos semanas que estuvo en Guam la pasó en compañía de Fritts y Rodda buscando serpientes, aparentemente de día y noche. En medio de las denuncias pro forma que más tarde consignaría, el escritor vislumbra la imposibilidad de erradicar la serpiente y cobra conciencia fundamental de la biogeografía como estudio de la difusión y distribución geográfica de las especies de vida. Insertaría una declaración de simpatía por *Boiga* y la exculpa por hacer lo que ha hecho la humanidad, extenderse por todo el planeta a expensas de las demás especies.

Haciendo cuentas el escritor confiesa que las excursiones posteriores al primer paseo periférico fueron infructuosas. En compañía de ambos guías inspeccionaron ochenta trampas dispuestas en los boscajes periferales de la base, con lagartijos caseros “gecko” (*Hemidactylus frenatus*) exótico común, de carnada viva. Pero las serpientes habían desaparecido. No había caído alguna en las repetidas búsquedas entre enjambres de telarañas que entorpecían el paso del aracnofobo confeso Quammen. La abundancia de arañas, descubre, se debe a la merma o desaparición de unas ocho especies de lagartijas nativas insectívoras. ¿Será que la serpiente *Boiga* también habría sido víctima de la bioacumulación de plaguicidas?

Se entera el escritor que el proyecto científico que encubre la misión de los herpetólogos es saber si la culpa es de la serpiente o alguna otra causa, menos el efecto tabú de la bioacumulación de plaguicidas. Sorprende que una especie exótica de esquinco (*Carla fusca*) introducida de Nueva Guinea en los años ’60 prospera contrario a las expectativas. En una última visita al laboratorio de entomología de la Universidad de Guam, los especialistas Nafus y Schreiner le aseguran que la isla está plagada de insectos exóticos que invaden continuamente por ser eje aéreo globalizado y entran en batalla campal con las especies nativas de insectos.

El escritor recogió sus bártulos y cortó por lo sano. Concluye abruptamente sus segmentos-capitulares “90” a “95” (págs. 321–342) dedicados al caso de Guam, y prosigue su libro con una disquisición especulativa sobre “cadenas tróficas” cuando la extinción de una especie conlleva la desaparición de muchas otras. Su carrera posterior ha sido exitosa. Refinado su estilo narrativo y uso del idioma se ha convertido en periodista favorito de la prestigiosa revista *National Geographic.*

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CERRO EL FARO: A CRITICAL COMPONENT FOR THE CONSERVATION OF NATURAL RESOURCES OF NORTHEASTERN PUERTO RICO

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Northeastern Puerto Rico is the richest natural sector of the island from the point of view of its biodiversity. There are two reasons why the northeast is biodiverse. One reason is that it contains all the climatic life zones of Puerto Rico. Nowhere else it is possible to travel from dry to rain forest (in the real sense of the word). The second reason is the topography. In a short distance from the ocean one can travel from sea level to over 1,000 m above sea level. The combination of climate and topography is critical for sustaining biodiversity because it creates gradients, which in turn provide opportunities for organisms to grow and diversify.

One element that adds to the biodiversity of the northeast is the ring of hills that occur between sea level and the Luquillo Mountains (Fig. 1, see hills in red). These low elevation hills or *cerros* provide topographic diversity on the lowlands and thus compliment the much taller Luquillo Mountains by adding environmental gradients within two of the six life zones of the region (Gould et al. 2007). These *cerros* are mostly moist and dry forests, depending on their geographic location, topography, and soil depth. An Institute draft document by Gould et al. 2010 (p.14) captured the importance of coastal hills for conservation in the northeast of Puerto Rico:

> "Coastal hills in Northeastern Puerto Rico cover nearly 6 % of the region. These harbor the coastal dry forests of the region and form a matrix of habitats, along with the mangroves and lagoons that are used by a number of wildlife species. The matrix of hills and wetlands make this one of the most biologically diverse components of the Puerto Rican landscape. Aside from a small area on the northeastern tip of the island these hills are virtually unprotected for conservation."

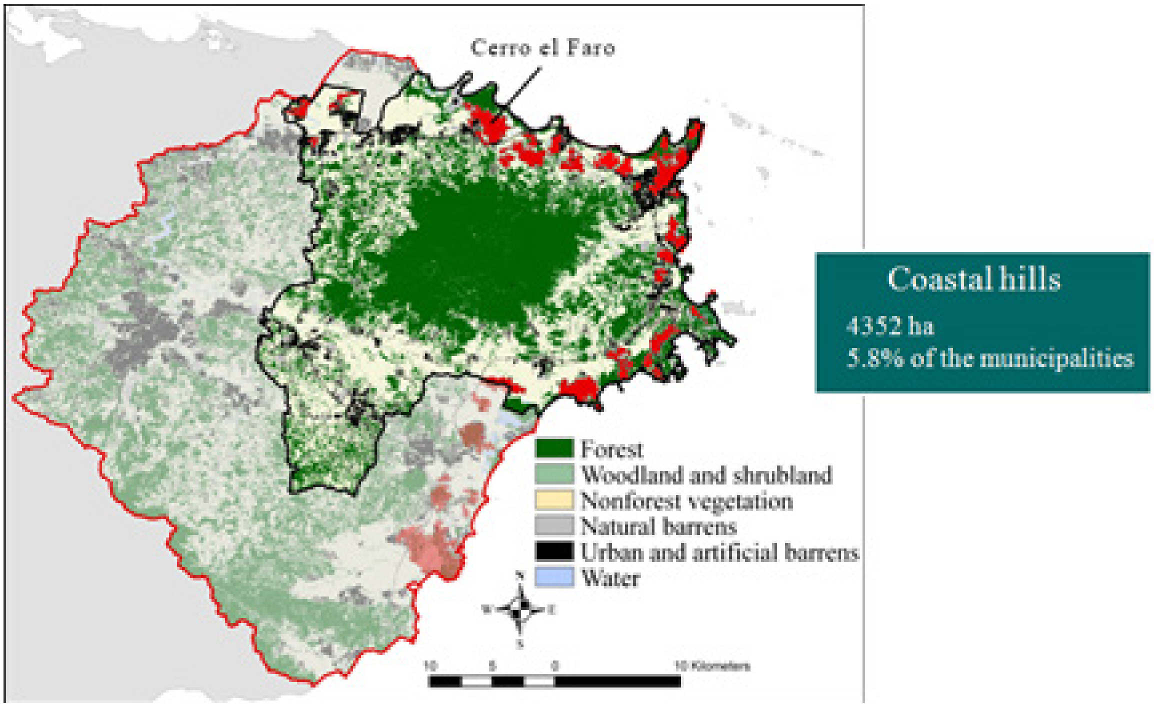
Gould et al. 2008 (p.10) have gone on to state:

> "We recommend expanded reserves in the coastal plain, particularly coastal hills and the matrix of wetland and upland vegetation; better regulation of development in the periphery of existing reserves to maintain the integrity of hydrologic systems in wetlands; and protecting viable corridors and buffer zones to connect the upland and coastal reserves."

Because these hills are mostly in the private domain, there has not been as much scientific attention given to them as there has been to other public areas of the Luquillo Mountains. However, recent observations at *Cerro El Faro* have convinced us of the importance of these coastal *cerros* in general and of *El Faro* in particular as conservation priorities.

Cerro El Faro is one of the largest hills and hydrologically connected in the system of coastal hills shown in Fig.1. Remarkably this *cerro* is connected to two of the most important rivers in northeastern Puerto Rico: the Río Mameyes and the Río Espíritu Santo, both critical watersheds of the El Yunque National Forest. Upon closer

Figure 1. Coastal Hills (in red) of Northeastern Puerto Rico and the location of Cerro El Faro. This map was created by the GIS Remote Sensing Laboratory of the International Institute of Tropical Forestry and was made available through William Gould and Maya Quiñones.



examination we found that the connection of *Cerro El Faro* with these rivers is hydrological, biological, and ecological. Streams and tributaries that originate at *El Faro* are part of the ecological and hydrological systems of Río Mameyes, Caño Rodríguez, and Río Espíritu Santo. This means that water, nutrients, organisms, and organic materials are freely exchanged between *El Faro*, the uplands of El Yunque, and the coastal plain, including the estuarine zone with its mangroves, freshwater wetlands, and other estuarine, benthic and marine coastal systems from *Punta Picúa* to the North East Ecological Corridor area.

Evidence of this connection and exchange between ecosystems is the presence of the freshwater and riparian crab, buruquena (*Epilobocera sinuaformis),* and the aquatic snail *Neritina virginea,* also known as the burgao. They evidence the connection and exchange between ecosystems. Massive migrations of the burgao have only been documented in the Río Mameyes and Espíritu Santo. This snail, observed in the *Quebrada Alonso*, a tributary of the Río Mameyes is a food source for aquatic birds such as the gallareta, (*Gallinula chloropus*) and for several of the larger predatory shrimp like the camarón bocú or palancú (*Macrobrachium* spp.) that are part of a complex aquatic and terrestrial food web that connects El Yunque National Forest, the Río Mameyes and thus the *Cerro El Faro* (Blanco and Scatena 2009, Blanco Libreros and Arroyave Rincón 2009). Recent studies identify this species as a biological indicator of river reaches and streams with physical and chemical characteristics associated with healthy forested landscapes. These snails are known to recover from and survive storms and flash floods in less than two months, but are negatively affected and take much longer to recover from stream substrate alterations like concrete embankments, shallow channels, culverts, and other channel works that modify flow (Blanco and Scatena 2005, Blanco and Scatena 2007). In addition to aquatic fauna there are also records of important terrestrial species. An example is the critically endangered Virgin Islands tree boa (previously known as the Mona boa, *Epicrates monensis granti*) present in the area of the *Cerro El Faro* which have been noted in current assessments by the Puerto Rico Department of Natural and Environmental Resources (Puente-Rolón 2001). Thus, protection of the vegetation in the *cerro* is also increasing the biological value of this site as habitat for this Federally listed endangered species (FWS 2007, Gould et al. 2008).

Of equal ecological and conservation importance is the vegetation of *Cerro El Faro*. We observed riparian zones with wetland indicator species and vigorous forests with significant native and introduced tree species. In addition, *Cerro El Faro* contains habitat that is suitable for rare tree species such as the cóbana negra (*Stahlia monosperma*) (García Bermúdez et al. 2005). This tree is a threatened and endangered species that is native to these coastal areas and wetlands (Fish and Wildlife Service 2007). We believe that by protecting the vegetation and land of *Cerro El Faro* from fires, deforestation activities, and other anthropogenic disturbances the original forest cover of *Cerro el Faro* can be rehabilitated if deemed necessary through purposeful management or by allowing natural ecological processes to do the job.

In summary, the conservation value and opportunity presented by *Cerro El Faro* is high because of its unique combination of topography, geographic position, and connection with both montane and coastal ecosystems, its functioning biota and its potential for rehabilitation (Gould et al. 2010). *Cerro El Faro* represents an ecological condition that is in short supply and when protected contributes to the overall ecological value of Puerto Rico.

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THE CARIBBEAN AND THE ANTHROPOCENE[1]

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Good day everyone. I am honored to be here with you as we recognize Jamaica's National Heroes and celebrate 75 years of accomplishments of the Forestry Department. I am also proud to be here in Jamaica, a land that has made us in the Caribbean proud for the way you have dominated the sprints at the Olympics and other world competitions. The Caribbean people are talented people and poised to lead the world as it is confronted with the consequences of the Anthropocene.

What? The Anthropocene? What is that! The Anthropocene is the era of human domination over the world. Human activity now dictates what happens in the world. What the climate will be, what species survive and which do not. How much freshwater we will have. How lands will be used. How much wilderness we will have, and so on.

Many are afraid of the Anthropocene. The Anthropocene is an era of uncertainty and some are afraid of what might happen in the future. Will many species become extinct? Will the climate change in ways that we cannot adapt to? How high will the sea level increase, and what will happen to all the cities and facilities that we have installed on our coastal zones? Will we lose our coral reefs, beaches and the tourists that visit us to enjoy those natural resources? As we travel into the unknown future we do so with trepidation and feel a little bit scared of what is in store for us, and our children.

However, I am not here to anticipate gloom and doom for our future. I am an optimist and I see many positive possibilities for us in the Anthropocene. You see, the era of human domination over the world has limits, it has an Achilles heel, and we in the Caribbean are poised to lead the world as it struggles with the Anthropocene. What is this Achilles heel of the Anthropocene?

The era of human domination over the world is dependent on oil. As humans we can do fantastic things with our technology, but to do so we need oil. We also live in the petroleum era, an era that is limited by oil reserves. At this historic moment we are approaching what has been called "Peak Oil" or the historic moment when we reach the peak in our consumption of oil reserves. From Peak Oil onwards, we will be using less and less oil because there will be less and less oil to extract and use.

To survive the Anthropocene we need strategies to deal with a declining oil supply

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1This is a speech in recognition of the 75th Anniversary of the Forestry Department of Jamaica delivered in October 31, 2013 at Kingstown, Jamaica. It is based on the following publication:

Lugo, A.E., E.H. Helmer, and O. Ramos-González. 2013. The greening of the Caribbean: from the taínos to the Anthropocene. The 9th Annual Public Lecture of the Environmental Foundation of Jamaica in Association with the Jamaica Protected Areas Trust/Forest Conservation Trust, Pegasus Hotel, Kingston, Jamaica. 32 p.

and thus a declining economic activity and declining technological capacity to support human activity. We are now at a time when humans begin to switch from oil to natural energies such as wind, solar, hydrological, and thermal. And guess what, we in the Caribbean have cultural and social capacity to survive in a world dependent not on oil but on natural energy resources.

Lets take a look at our beloved Caribbean. I want to focus on four big things happening in the Caribbean regarding our natural resources.

- First of all, the Caribbean is a "Hot Spot" for organisms, both marine and terrestrial. A Hot Spot is a region of the world with disproportionate quantities of unique biodiversity, meaning plants, animals, microbes, and the ecosystems they form. This means that over 20 percent of the species we see in the Caribbean are unique (or endemic) to the Caribbean, they occur nowhere else in the world.
- Second, the flora and fauna of the Caribbean has been enriched by the introduction of plants and animals by humans. Today, the biodiversity of the Caribbean is much more richer than it was when the first humans arrived in the region.
- Third, the Caribbean is one of the few places in the world where the area covered by forests is growing. Today, we have more forest cover than anytime before in over a hundred years. So we are greener!
- Finally, the forests and ecosystems emerging in the Caribbean after the agricultural era are what we call novel forests, because they are composed of a combination of plant and animal species that is different from the historical ecosystems that preceded them before the deforestation that occurred over a hundred years ago. Those species introduced by humans have recombined with the native species of the Caribbean to form these novel ecosystems. Moreover, these novel forests are adapted to human activity because they are a product of human activity.

In summary, the Caribbean is greener than it has ever been, it contains more species of plants and animals than it has ever had, it harbors ecosystems that are different from those that were present before humans, but it maintains pristine native ecosystems with their unique biota therefore conserving the Hot Spot of biodiversity for which we are globally known.

But the greatest surprise for us in the region is that the Anthropocene, particularly after Peak Oil, requires that humans depend more and more on natural resources, and regions with sound stewardship of their resources will find themselves ahead of those who have squandered their resources. Forests acquire new values in the Anthropocene. They provide what we call ecological services that clean our water and assure abundant supplies of this vital liquid. They serve as green infrastructure, particularly in cities where trees moderate temperatures and lower the electric bill of those who have air conditioning. Well-placed and maintained urban forests help reduce criminal activity and provide places where people can relax and lower the daily stress. And now we know that forests store carbon that help moderate the global climate and countries can now receive carbon credits for allowing their forests to grow and not be depleted.

All four natural resources characteristics of the Caribbean, including its forests, are essential for coping with the Anthropocene and leading the world in the era after Peak

Oil. But they are not enough. There are still four other aspects of the Caribbean that must be added to the stew of Anthropocene success.

- First, Caribbean people are inherently conservationists. One reason the biodiversity Hot Spot of the Caribbean and the native pristine forests in the Islands have survived deforestation and high population density, is because the people made it so. Caribbean people depend on nature for survival and they understand the importance of conservation. Jamaica was called the Island of wood and water because of its richness in these resources, which were valued by its indigenous populations and continue to be treasured by the present population.

- Second, Caribbean people embrace diversity and novelty. We love equally the native *Lignum vitae* and *Hutias* as we do the introduced mango or breadfruit tree. We benefit from all biodiversity and value all of it.

- Third, We are a people of diverse culture and beliefs, with well-organized democratic governments and manage to somehow to live up to the motto of Jamaica: *Out of Many, One People*. As one people, we also accept science as a source of understanding and objective information for policymaking and development of regulations.

- Finally, we function as a social ecological system, each Island according to its social and ecological circumstances. Nevertheless, the connection between the social and ecological systems of the Caribbean is what provides the power of adaptation for the Anthropocene. An adaptation that will propel the Caribbean to a global leadership position for dealing with the decline of the world's fossil fuels after Peak Oil.

As we celebrate the 75th anniversary of the Forestry Department and recognize the achievements of your Island Heroes, we must reflect about the future of our Caribbean. Here is my reflection: The Caribbean has evolved considerably over the millennia adapting and evolving as necessary to survive in a changing world. We experienced the Taínos, the Europeans, deforestation, agricultural monocultures, land degradation, urbanization, hurricanes, and now as the world recognizes the Anthropocene, we realize that we have been living in the Anthropocene for a long time because the Islands have been densely populated and surviving on their own for many centuries before modern technology connected us to the whole world. Today, we have beautiful landscapes and we are wiser than before because although we have abused the land, the land has been sufficiently resilient to allow us to witness its recovery while we live off the fossil fuel reserves.

Ah, but the oil is being depleted and we might need to go back to depending on the land. Will we be smarter the second time around? Or will we make the same mistakes as before?

As an optimist I say we will do better because we are wiser and we now know how important the land and natural resources are to our survival. We can feed off our cultural heritage and our close connection to the biota to develop social ecological systems that will allow us a prosperous livelihood as the Anthropocene comes to an end. What are the things we must do to be successful in the post Peak Oil era?

We must be people oriented, focus on the quality of life, on the better good for everyone, we need to make our cities livable by adding trees because that is where most people congregate. Urban forests and green infrastructure are important components for making the city livable. We must concentrate conservation activity on all lands so that we may address issues of food security as well as environmental quality. Our governance and conservation processes must be transparent, collaborative, and inclusive. Basically all lands and all hands have a role to play.

Caribbean Islands can do what we need to do because we have done it before and we now know better to make the future be a prosperous one for everyone. We will lead the world as we have done in the past when the world interest was in our natural bounties. In the future we will lead because of our understanding of how to live off the land without destroying its capacity to support us.

May the Forest be with you!

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LOS CAÑAVERALES DEL PASADO Y LAS AGROINDUSTRIAS DEL FUTURO

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La administración pública del presente se propone revivir el éxito del gobierno Borbón, déspota e "ilustrado" de los Siglos 18 y 19 que estableció la siembra de caña de azúcar con mano de obra esclava. Ahora no serán esclavos, según la Secretaria de Agricultura Myrna Comas, sino maquinistas en cabinas con aire acondicionado y al son de reggaetón. Los llanos más productivos del pasado en Ponce, Aguada y las vegas no urbanizadas del norte y este volverán a serlo. ¿Habrá un plan "modelo" para salvaguardar la posteridad de las tierras mecanizables de la codicia desarrollista?

Cuando se desinfle por inverosímil el balón neo-borbón se podrán considerar cultivos y crianzas para producir materias primas más útiles que el melao para el desarrollo agroindustrial del país. El pasado podría ser tprólogo. Nuestros aborígenes usaban los mismos llanos para conucos extensos de yuca (*Manihot esculenta*) que hoy día se siembra mundialmente para materia prima alimenticia de humanos y animales domésticos. El arroz de secano (no necesita encharcamiento) alimentaba la población del Siglo 18. La ganadería vacuna de entonces podría modernizarse para convertir la Isla en la Holanda de quesos del Caribe.

En tiempo mucho más reciente la introducción experimental de especies forestales por el instituto federal de silvicultura tropical aportó selecciones prometedoras para bosques cultivados como ha propuesto el dasónomo emérito Frank Wadsworth. Tenemos huertos de especies como la teca (*Tectona grandis*) que supliría una industria de muebles finos, se adapta bien y es cultivada mundialmente. Hay aquí especies de *Eucalyptus* que podrían producir bosques densos cultivados para pulpa de papel, cartón y "plywood" en cinco años, como se hace en Brasil y otros países de América. Otra especie exótica que compite con los Eucalyptus en crecimiento rápido es el kadam (*Neolamarckia cadamba*) cultivada mundialmente para madera prensada, y se ha establecido con éxito aquí.

Pero hay otras especies de plantas con potencial agroindustrial por su productividad excepcional de biomasa útil como materia prima. Los cañaverales de palmas rattan (géneros *Calamus* y *Daemenopsis*) suplen una economía multimillonaria de muebles y exportación de materia prima en Las Filipinas. Otras palmas tropicales de aspecto convencional producen aceites que compiten con el de oliva en atributos de calidad y utilidad. El fruto de la palma africana de dendé (*Elaeis guineensis*) rinde un aceite de cocina y consumo de creciente demanda por su falta de "trans-fats". La palma suramericana de seje (*Jessenia bataua*) produce un aceite física y químicamente similar al de oliva y se utiliza además en cosméticos y productos farmacéuticos. El arbusto amazónico de sorba (*Couma utilis*) produce un abundante látex potable como leche vegetal, y sirve para fabricar goma de mascar y otros productos orgánicos. Se exporta a países industrializados pero aún no hay huertos intencionales.

Otros tipos de plantas ofrecen posibles cultivos extensivos de alta productividad de materia prima industrial. Las bambúas del género *Phyllostachys* son cultivadas intensamente en China y Japón para una variedad de usos. En Estados Unidos los intereses madereros han bloqueado su cultivo para impedir la competencia. El cultivo de matojos parientes de la yuca en la familia de las *Euphorbacia* que rinden latex procesable a biocombustible se encuentra en desarrollo tecnológico avanzado.

Falta mencionar el cultivo de uvas tropicales (*Vitis x vinífera*) para vino, jugo, vinagre y destilado en aguardiente. El mercado local para los productos vitícolas es tan grande que hay que preguntarle a Roberto Serrallés si no se ha equivocado de cultivo. El melao se produce en países hermanos mucho más barato que aquí, y las multinacionales del ron obtienen la materia prima en los mismos sin necesidad de subsidio por nuestro erario en bancarrota.

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