POST-HURRICANE GROWTH AND RECRUITMENT OF PLANT SPECIES USED BY BIRDS IN NORTHERN PUERTO RICO

By

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ABSTRACT

In this work, I studied the effects of natural disturbances, specifically Hurricane Georges, on plant growth and survival in forests of north-central Puerto Rico. Eight study plots were monitored from February 1999 to January 2000. This study demonstrated that seedling density of many species was higher in disturbed sites. Two hundred and seventy-nine new seedlings germinated, 9.36 % of the total individuals recorded in all study plots (2,981). Growth (basal area, ht) for all species combined was significantly greater in disturbed sites. Survival of seedlings was consistently higher in disturbed plots. Seedlings that germinated post-hurricane and their species richness were higher in disturbed plots. Species richness highlighted the role of neighboring parental trees, as well as the seed bank and dispersal. Forest gaps facilitated germination, and possibly the replacement of plants otherwise inhibited by canopy species. Lessons gained from my study should be useful to promote native plant species regeneration, and aid in reconciling competing forest management practices.

RESUMEN

En éste trabajo, estudié los efectos de los disturbios naturales, específicamente del Huracán Georges, sobre el crecimiento y supervivencia de plantas en los bosques de la parte norte –central de Puerto Rico. Ocho parcelas fueron seguidas de febrero de 1999 a enero de 2000. Este estudio demostró que la densidad de plántulas de muchas especies fue más alta en áreas con disturbios. Un total de 279 plántulas nuevas germinaron, 9.36 % del total de individuos marcados en todas las parcelas de estudio (2,981). El crecimiento (área basal, altura) de todas las especies combinadas fue significativamente mayor en áreas de disturbio. La supervivencia de las plántulas fue consistentemente mayor en parcelas con disturbio. La germinación y la riqueza de especies fue mayor en áreas con disturbio. La riqueza de las especies resaltó la contribución tanto de los bancos de semillas como su dispersión. Los claros en los bosques facilitaron el reclutamiento y posiblemente el reemplazo de plantas que de otra manera serían inhibidas por el dosel. Los conocimientos adquiridos de mi estudio pueden utilizarse para promover especies de plantas nativas, y ayudar a combinar prácticas de manejo forestales que pudieran parecer incompatibles.

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CHAPTER I

INTRODUCTION

Hurricanes are common, but potentially highly disruptive events for ecosystems in the Caribbean (Tanner et al. 1991). These disturbances can have significant effects on plant recruitment and plant and animal interactions (e.g., Waide 1991, Perez-Rivera 1991, Wiley and Wunderle 1992, 1993; Wunderle 1999, Collazo et al. 2003). Yet, these environmental perturbations are a vital part of Caribbean ecosystem dynamics (Pickett and White 1985, Sousa 1984). Succession following hurricanes has long been the subject of analyses and discussions. In trying to account for post-perturbation successional changes, Engler (1954) proposed two models, namely, the relay floristic and initial floristic composition models. The relay floristic model proposes that there is an initial establishment of pioneer trees followed by the succession of a different suite of secondary species, which arrive later. In contrast, the initial floristic composition model proposes that the same pool that existed immediately after the hurricane is the source of the regeneration. Patterns of post-hurricane succession have been documented largely for island floras (Lugo et al. 1982, Wadsworth and Engler, 1959, Walker 1991, Weaver 1986, 1989). These studies generally provide evidence in support of both models of succession.

One of the most notable effects of hurricanes is the creation of forest gaps. Gaps are a critical type of disturbance, initiating the forest growth cycle (Whitmore 1975). Following a disturbance, saplings and seedlings growing from the forest floor compete with the recovery of forest canopy from the trunks and branches of surviving trees. The number of these seedlings and saplings that will reach the forest canopy depends on the severity of canopy damage and the rate of canopy recovery (Tanner et al. 1991). Gaps increase light penetration, air and soil temperatures, and decrease relative humidity compared to closed canopy (Denslow 1987). Increases in light following a hurricane accelerate the growth of herbs and saplings of pioneer genera such as *Cecropia* and *Didimopanax* (Fernandez and Fletcher 1991). Treefall gaps therefore may favor establishment of species not normally found in the understory of shaded forest (Putz 1983, Peterson and Pickett 1990, Carlton and Bazzaz 1998).

In the last decade, Puerto Rico has been hit by two major hurricanes, Hugo and Georges, the latter on 21 September 1998. Unlike Hugo, Georges traversed the island on an east-west axis, impacting interior forests, such as those in north-central Puerto Rico. This event provided a unique opportunity to assess not only its impact, but also the pattern of recovery of these interior forests. Lessons learned from assessments of naturally disturbed areas would also be valuable to predict the benefits of creating gaps, or openings in managed forests such as Rio Abajo Commonwealth Forest. The Rio Abajo Forest has been targeted for establishment of the second population of Puerto Rican Parrots (USFWS 1999). Parrots are frugivores; therefore, studies of post-hurricane plant dynamics could provide valuable insights for promoting selected plant species (e.g., food resources), and aid in reconciling competing forest management practices (e.g., habitat enhancement for avifauna and silviculture).

In this work, my goal was to gain a better understanding of the effects of natural disturbances in forests of the north-central region of Puerto Rico. This region contains a mosaic of forests spanning across volcanic and karstic geologic formations. My working hypothesis was that forest disturbance caused by hurricanes influences seedling growth and survival. To address this possibility, I determined if seedling species composition differed between disturbed and undisturbed areas and whether gaps (i.e., disturbed sites) created by the hurricane promoted faster growth and survival rates among selected plant species. These questions were addressed using a paired-sampling scheme whereby study plots were established in disturbed and undisturbed areas in the aftermath of hurricane Georges. Special attention was paid to plant species that serve as food resources to avian frugivores in the region, including those used by the Puerto Rican Parrot (*Amazona vittata*). Plant species of interest included *Schefflera morototoni*, *Cecropia schreberiana*, *Guarea guidonea*, *Cordia sulcata*, *Inga vera*, *Inga fagifolia*, *Casearia silvestris*, *Casearia decandra*, *Caseria guianensis*, *Casearia arborea*, *Ocotea leucoxylon*, *Ocotea floribunda*, *Clusia rosea*, *Miconia prasina*, *Miconia serrulata*, and *Andira inermis* (Cardona et al. 1986, Snyder et al. 1987, Collazo and Groom 2000, Carlo et al. 2003, Carlo et al. In Press). In all, 16 species were selected. These plant species met one of the following three criteria: 1) were consumed by nearly all frugivores in the region (Saracco 2001; Carlo et al. 2003, Carlo et al. In Press), 2) were preferentially consumed (i.e., important to selected members of the avian community; Carlo et al. 2003), or 3) were known to be consumed by Puerto Rican Parrots (Cardona et al. 1986, Snyder et al. 1987).

CHAPTER II

REVIEW OF LITERATURE

The rate of seedling and sapling growth and survival is dependent on the rate of canopy recovery, the size of gap and the level of damage (Brokaw 1987). Hurricanes cause massive disturbances in forests, and as such can have enormous impacts on forest dynamics. The effects of hurricanes have been studied for decades in the tropics. In 1956, Wadsworth and Engler studied the effect of Hurricane Betsy on Puerto Rico's forest. They found that the most general type of damage was defoliation and the breakage of the limbs. Indirect effects were less spectacular, but just as lethal. For example, sun scalding of limbs caused the subsequent death of trees. The extent of damage depended on site characteristics such as elevation, topography, aspect, and forest conditions. Wadsworth and Engler (1959) also found that different trees varied significantly with respect to their susceptibility to windthrow and breakage from hurricanes. In the subsequent paragraphs, I summarize the most important work related to hurricane damage and its effects on forest structure.

Brokaw and Walker (1991) summarized data on effects of Caribbean hurricanes on vegetation. In most cases, there were radical changes in the physical structure of the forest. Mortality, accelerated growth, and differential germination and recovery from damage altered population abundance and size structure. Their overview confirmed the findings of Wadsworth and Engler (1956), as most studies reported that the principal type of damage was defoliation. Moreover, they established that large trees were more susceptible to direct damage than small trees. Where large trees sustained damage reduced upper canopy cover considerably. The damage was greatest on slopes facing the wind and on level areas where the wind blew unimpeded. Another important finding was that while damage was extensive, tree mortality was not. Most tree populations exhibited rapid recovery.

Walker (1991) established that the decrease in overall canopy height caused by hurricanes increased the light that penetrates the understory. This increase promoted colonization and growth of pioneer species and accelerated growth of vegetation regeneration already present in sites (You & Pettty 1991). Sunlight patterns were critical for germination. For example, the germination of *Cecropia schreberiana* and *Schefflera. morototoni* likely depended of the light intensity that plots received. These two pioneer species had smaller seeds. Generally, light demanding species have smaller seeds than do more shade tolerant species and are able to maintain dormancy for long periods of time in the soil under an intact forest canopy and germinate in response to increases in incidental radiation and in temperature (Hopkins and Graham 1983, Marquis et al. 1975, Foster 1987). *Schefflera morototoni* will be able to maintain dormancy for longs period of time due to it hard seed coat (Liegel 2000), but *Cecropia shcreberiana* was unable to maintain its viability for long time (Silander 1979). Sunlight at the forest floor may be less than one percent of the top of canopy, but various size gaps can increase this substantially. Plants and seeds in the understory have a range of light requirements (Chazdon 1988). Some are capable of growing and maturing in dense shade of a mature forest, such as large-seeded species of the Lauraceae. Garwood (1983) and Becker (1985) reported that shade tolerant species have shorter dormancy capacities as seeds but high shade tolerance as seedlings. Shade tolerance may lead to a kind of suspended animation until gaps in the canopy give them at least a brief access to the sunlight that is crucial for growth (Pompa and Bongers 1988).

Lugo et al. (1983) documented the damage to forest in Dominica in the aftermath of Hurricane David. Damage was more severe on the exposed and flat highland areas where the canopies completely disappeared in some regions. Data analyses suggested that complex vegetation (e.g., diverse associations) was more resistant to hurricanes damage than simpler vegetation associations (e.g., where the dominant vegetation were palms). Trees in larger diameter classes tended to uproot with more frequency than the smaller diameter trees, which tended to snap.

Hurricane disturbances also affect plant growth and survival through induced pulses of litterfall (Bruederle and Stearns 1985). Lodge et al. (1991) reported fine litter deposit on the forest floor during Hurricane Hugo that was 400 times the average daily input at Bisley and El Verde, and 682 times at East Peak in the Caribbean National Forest, Puerto Rico. The physical effects of such massive inputs of litter can affect seedling germination and survival (Guzman–Grajales and Walker 1991). Litter can act as a mechanical factor that damages and /or kills plants (Clark and Clark 1989) and can modify the conditions of microsites (e.g., humidity, nutrients and light availability) in which seeds germinate and seedlings establish (Vitouseck 1984, Vazquez–Yanes et al. 1990). Guzman et al. (1991) showed that the density of seedlings was highest in areas where litter was removed experimentally when compared to controls, confirming the hypothesis that the litterfall inhibits seedling germination. Lodge et al. (1991) found that total nutrient input to the forest floor from hurricane litterfall was between 1.3 and 3.0 times the annual litterfall transfer at Bisley and El Verde. Additional nutrients, which were retained temporarily in suspended loose litter, broken crowns, and uprooted trees accounted for 48 to 56 percent of hurricane litter nutrient transfer at El Verde. The flux of nutrients associated with this litter apparently altered nutrients cycles (Steudler et al. 1991) and may have affected soil nutrients availability and forest productivity (Sandfort et al. 1991). Lodge (1991) reported inputs of phosphorus in the leaffall 2.5 times the normal annual input of phosphorus in leaffall at East Peak in the Caribbean National Forest. Such high magnitude of transfer to the forest floor may affect soil fertility (Sandfort et al. 1991), and subsequently plant survival growth.

The soil seed bank is critical to understanding the role of buried seed in forest generation in tropical forests (Butler and Chazdon 1998); yet, the response of soil seed bank to large-scale disturbances, such as hurricanes, is not well known. Some studies have suggested that seeds already stored in tropical forest soils are an important source of germination following a disturbance, and influence the course of forest regeneration and secondary succession (Young et al. 1987, Swaine and Whitmore 1988). Viable seeds in the soil can be a major source of recruitment for plant communities (Cheke et al.1979, Fenner 1985, Swaine and Hall 1983). Soil seed banks show both seasonal and annual fluctuations (Guevara and Gomez- Pompa 1976, Gross 1990, Dalling et al. 1997, 1998), as well as spatial variation in species composition and abundance (Thomson 1992).

There are only a few studies of disturbance and recovery for mesic forests on limestone. Rivera and Aide (1997) assessed forest recovery in abandoned pastures and coffee plantations. They found that abandoned pastures had a higher diversity and density of woody species than the abandoned coffee plantations. In pastures, *Spathodea campanulata* was the dominant species, where as in coffee plantations it was *Guarea* *guidonea*. Seedling composition in coffee plantations suggested that there was a resistance to change in terms of dominant species. For example, seedlings of *S. campanulata* did not rank among the top 10 most abundant species in coffee plantations because the species was not tolerant to shade. Rivera and Aide (1987) analysis suggested that *S. campanulata* adults would be replaced by shade tolerant species like *Guarea guidonea* and *Andira inermis.* This study also showed that forest patches that remained in the steep slopes of limestone would facilitate the recovery of adjacent forests, at least where bats were the important seed dispersers. In addition to this work, many others have shown that historic land use will affect regeneration and continue to affect forest dynamics for many years (e.g., extensive studies by Foster 1987 in Massachusetts).

The karst region of Puerto Rico, and specifically the Rio Abajo Forest, has been identified for the reintroduction of the Puerto Rican Parrot in an effort to minimize the chance of extinction of the species by establishing a second population outside the Caribbean National Forest (White et al. 2000). Forests in this region contain many of the food plant species used by parrots (Cardona et al. 1986, Collazo and Groom 2000). The Rio Abajo Forest was established in 1935. There are 18 types of soils found within the forest; however, the majority of them are of little importance except the rocky karstic soil, a Soller complex that occupies 82.2% or 1869.7 ha of the forest (DRNA 1986). Most of the Río Abajo Forest (89%, or 2037.9 ha) is found within the subtropical moist forest life zone (Ewel and Whitmore, 1973). The mean annual rainfall is 2000 mm/year. A high percentage of the forest soil has been used for silviculture. The Civilian Conservation Corp (CCC) established *Calophyllum antillanum* and *Swietenia mahogany* plantations between 1936 and 1938. Afterwards, in 1977, plantations of *Swietenia macrophylla*, *Tectona grandis* and *Hibiscus elatus* were established.

Releases of Puerto Rican Parrots in the Rio Abajo Forest are scheduled for 2006 and preparations include short and long-term planning processes and documents. Among them is the revision of the Rio Abajo Forest Management Plan (J. A. Collazo, North Carolina State University, pers. comm.). This plan will incorporate specific management practices (e.g., gap creation, tree plantings, harvest restrictions), which presumably will benefit the reestablishment of the parrot population and foster the presence of other members of the avian frugivore community. Ultimately, the Department of Natural and Environmental Resources wants to have protocols in place to monitor management scheme effectiveness, and if need be, adjust (i.e., adaptive management).

Few studies in Puerto Rico have been designed to examine the dynamics of floristic components with the goal of improving habitat for the avian community. The connection between selected plant species and avian use is reported primarily as check lists (e.g., Leck 1972, Pérez-Rivera 1991, 1994). Supplemental information comes from observations made during plant population dynamic studies (e.g., Silander 1979). The few examples of more in-depth studies designed to establish frugivore-resource relationships are associated with endangered species (e.g., Puerto Rican Parrot [Cardona et al. 1985, 1986; Snyder et al. 1987], Yellow-shouldered Blackbird [Mckensie 1989]). For example, Cardona et al. (1986) evaluated the availability of 23 plant species that were either known to be, or could be food plants for the Puerto Rican Parrot or Puerto Rican Plain Pigeon (*Columba inornata*) in the Rio Abajo Commonwealth Forest.

The work by Carlo (1999) and Saracco (2001), and their publications since (Carlo et al. 2003, Saracco 2004, Carlo et al. In Press, Saracco In Press), are recent examples of in-depth frugivore-plant resource studies in Puerto Rico. They are of particular value to guide habitat management in north-central Puerto Rico because they were aimed at discerning resource use patterns under a number of circumstances and across the landscape. For example, Carlo et al. (2003) identified plant species used preferentially across karstic and lower montane forests of north-central Puerto Rico. Saracco and colleagues, on the other hand, examined factors that might influence the use of plant species such as composition of plant neighborhoods (Saracco et al. In Press), or their spatial arrangement (Saracco et al. 2004). These findings are useful to planners because they identify a number of resources commonly used within and across forest types, and begin to place their use in a seasonal and spatial context. Moreover, they begin to set the foundation to better interpret the impact of habitat alterations on avian diets (i.e., shifts, Carlo et al. 2003, Carlo et al. In Press), bird-plant interactions pertaining to pollination and seed dispersal (Jordano 1987, Carlo 1999, Saracco 2001, Jordano 2003), and survival and reproduction of avian species (Morrison et al. 1998). These data become more critical when the landscape has been altered markedly, as historical forest data indicate for Puerto Rico (Wadsworth 1959, Little et al. 1974). Clearly, any effort aimed at preserving Puerto Rico’s avifauna must also include reliable information on plant demographics and factors affecting their abundance and distribution. This is the main thrust of my work.

CHAPTER III

STUDY AREA

This work was conducted in four study areas located in forests occurring on volcanic and karstic soils in the north-central region of Puerto Rico (Figure 1). In areas of volcanic soils, one study area was in lower montane forest (Tres Picachos) and another in an active coffee plantation (Cialitos). In the karstic region, one study area was established in the Rio Abajo Forest and the other in an abandoned coffee plantation (Frontón). These study areas were monitored from February 1999 to January 2000. Study areas were selected based on availability because the damage from hurricane Georges (September 1998) was extensive in the region, but spatially heterogeneous. It also includes the Rio Abajo Forest, an example of karstic forest, due to the importance of this site for reintroduction efforts for the Puerto Rican Parrots (planned in 2006).

Recognizing that available study areas were diverse, but suitable to the fundamental questions of my study (i.e., impact of natural disturbances), I established paired plots (2 x 50 m) within each study area, one in a section markedly disturbed by hurricane Georges, and the other in an unaffected, but adjacent area. A brief description of each study site within each study area and the location of each site are presented below.

1) **Study area in Frontón, Ciales** –Limestone Soil (karstic)

Description of disturbed site: The plot was established in the east slope of a mogote. Eighty percent of this plot was damaged. This included uprooting, snaping, and defoliation. Before the hurricane hit the site *Guarea guidonea, Calophyllum antillanum*, *Sapium laurocerasus*, *Thouinia striata var striata* and *Ocotea floribunda* were the dominant trees in the plot (personal observations). After the hurricane, only shrubs and some trees of *Thouinia striata* and one *Calophyllum antillanum* remained with little damage. Vines and thickets dominated the most affected parts of the plot, where the pioneer species *Cecropia schreberiana* was established. The study site was located in Barrio Frontón, Sector Máximo Nuñez, Camino Los González. P.R. 146, Km.16.3 Interior, north of the road, 18° 18' 671 N, 066° 32'595W, elevation 710 m.

Description of undisturbed site: The plot was established in the foot of the western slope of a mogote. The foot of this mogote was characterized by deep soil where large and tall forest trees are present. These included *Sapium laurocerasus*, *Hyeronima clusioides* and *Thouinia striata* var *triata*, all of which reach a height of more of 20 m. The canopy is closed, dominated by species such as *Guarea guidonea* and *Calophyllum antillanum.* The understory is open with a diverse species composition but few individuals of each. The site contained species typically found in limestone forests, classified as evergreen humid forest. The study site was located in Barrio Frontón, Sector Máximo Nuñez, P.R. 146, Km. 16.3 interior, north of the road, 18° 18' 686 N, 066°32' 585 W, elevation 332 m.

2) **Study area in Cialitos** (abandoned shade coffee plantation) – Volcanic Soil

Description of disturbed site: The plot was established on a slope, close to the top of a hill. Over 50% of the canopy was affected by the hurricane. The damage to trees included uprooting, snaping and defoliation. The vegetation within it was a mixture of secondary species and some remaining primary species. Some of these primary species were *Dacrioydes exselsa*, *Tetragastris balsamifera* and centenary species of *Magnolia portoricensis* and *Buchenavia capitata*. There were also some naturalized exotics species such as grasses, *Passiflora edulis* and *Syzigium jambos*. The most abundant seedlings in the undersory were *S. jambos*. Vines and herbaceous species were dominant in the two extremes of the plot were the most damage occurred. The study site was located in Barrio Cialitos, Sector Las Cruces, P.R. 608 Km7.7, 18° 14'541N, 66° 31' 871W, elevation 710 m.

Description of undisturbed site: The vegetation in the undisturbed plot was secondary, yet late enough in successional stage that species diversity was very high. There was no evidence of any agriculture activity in this plot, although the exotic species *Syzigium jambos* is very common, indicating prior use as a shaded coffee plantation. The native species *Tetragastris balsamifera* and bromeliads were also common. Many species of native ferns grew along the edge of the plot. The dominant species in the understory were *Psychotria berteroana*, *Syzigium jambos* (dominant species) and *Miconia prasina*. The study site was located in Barrio Cialitos, Sector Las Cruces, P.R. 608 Km7.7, 18° 14'374 N, 66° 31'805W, elevation 630 m**.**

3) **Study area in Tres Picachos** – Volcanic Soil

Description of disturbed site: The plot was established in a damaged area surrounded by high canopy. Practically all trees had fallen in the aftermath of hurricane Georges, except for two trees of *Guarea guidonea.* However, both were defoliated and most branches were broken. Species such as *Guarea guidonea*, *Inga laurina*, *Cecropia schreberiana*, *Piper glabrescens* and *Mussa sapientum* were the dominant species surrounding the plot. *Mussa sapientum* was present and a remnant from past cultivation. Vines of the genus *Ipomea sp.* were noticed growing over the schrubs. The study site was located in Barrio Toro Negro, P.R 533 Km 2.8 south side of the road, 18° 13'764 N, 66° 32' 430 W, elevation 651 m.

Description of undisturbed site: The plot was established in the foot of the mountain known as Tres Picachos. *Guarea guidonea* was the dominant species. The remaining species were typical of humid forests and primary forests. These included *Buchenavia tetraphylla*, *Cinnamomun elongatum*, *Miconia serrulata*, *Ocotea leucoxylum* and the fern *Cyathea tenella*. Exotics species such as *Mussa sapientum*, *Citrus paradisii*, *Hibiscus rosa-sinensis*, *Coffeea arabica* and *Mangifera indica* were present and considered remnants from past cultivation. The canopy was closed and tall, as a result the understory was open with few shrubs. The study site was located in Barrio Toro Negro, P.R 533 Km 2.8 south side of the road, 18° 13'819 N, 66° 32' 359 W, elevation: 621 m.

4) **Study area in Rio Abajo Forest** – Limestone soil (karstic)

Description of disturbed site: The plot was established on the edge of a *Tectona grandis* plantation in the base of a mogote. The forest in this area was a mixture of some native species like *Hyeronima clusioides*, the rare species of palm *Aiphanes acanthophylla*, *Pseudolmedia spuria*, and exotics species such as *Tectona grandis, Casuarina equisetifolia*, *Annona muricata* and *Persea americana*, all remnants of past cultivation. As a consequence of the hurricane, species of rapid growth, such as *Piper glabrescens*, *Xanthosoma sp.*, *Miconia laevigata*, *Gonzalagunia hirsuta*, *Solanum torvum*, ferns and vines, were common and covered practically the entire understory. The study site was located in Barrio Río Arriba, Rio Abajo State Forest, P.R. 621 km. 9.2 north side of Road, 18° 19'852 N, 066° 42' 960 W, elevation 337 m.

Description of undisturbed site: A plot was established near a *Hibiscus elatus* plantation, which had been thinned during the 1970's. The remaining trees were 2 m apart in the center of the plantation and widely spaced as the plantation extended onto the mogote slopes. The canopy was closed and the trees reached a height of 18 m. The vegetation in the center of the plantation was very scant, but also very diverse. *Calophyllum antillanum* was the most abundant species, especially where light conditions did not permit the germination of others species. Germination and diversity of species was greater where the distance between *Hibiscus* individuals was more than 2 m. In those areas, species like *Psychotria brachiata*, *Miconia prasina*, *Miconia laevigata*, *Picramnia pentandra* and the vine *Forsteronia portoricensis* were common. The study site was located in Barrio Río Arriba, Rio Abajo State Forest, P.R. 621 km. 9.2 north side of Road, 18° 19’900 N, 066° 42’ 954 W, elevation 324 m.

CHAPTER IV

METHODS

Two plots (2 m x 50 m) were established in each study area, one in a section strongly disturbed by hurricane Georges, and the other in an unaffected area. The undisturbed plots had closed canopy, and no damage to any nearby trees from the hurricane. In contrast, all disturbed plots were embedded in large gaps with more or less continuous area of open canopy, and widespread evidence of recent tree throw, trunk breakage and limb loss. Live trees and shrubs were identified to species to determine species composition of each plot. Because the resulting sample size was too small to characterize the diversity of each study area, two additional plots (10 m x 50 m) were placed adjacent to each plot, and I identified all live trees and shrubs > 3 cm DBH in these additional areas.

Seedling composition was sampled in ten randomly chosen 1 m^2 quadrants within each plot. On each visit, all woody seedlings (< 10 cm tall, excluding vines) and saplings (10-100 cm tall) were permanently labeled with aluminum tags. Data were expressed as the total number of seedlings (or seedlings, when looking at the youngest recruits alone) summed over all quadrants (10 m^2 total) and mean density per quadrant (per m^2). To look at the fate and performance of new seedlings, I tagged and measured new recruits, defined as new seedlings that had obviously recently emerged in my first census, or as ones that had germinated since the last census. The fate (survival) of each of marked seedling was followed over three sampling occasions or nearly a year (February 1999, July 1999, January 2000). Survival was expressed as the probability that a seedling marked at the beginning of the study (February 1999) was alive at the end of the study (January 2000). I analyzed survival data using Program MARK (White and Burnham 1999), treating seedlings marked in the beginning of the study as the cohort and the other two sampling occasions as recapture periods. Because plots were censused on every occasion, counts were complete. I ran these analyses only for those species with enough data to run parallel tests on growth. Otherwise, data are expressed as proportion of seedlings alive at the end of the study. I ran Z-tests to compare survival probabilities between disturbed and undisturbed sites. Estimates of seedling growth were obtained from the difference in height and basal diameter between the beginning (February 1999) and the end of the study (February 2000). Trees and shrubs with > 3 cm diameter at breast height (dbh) and > 1 m tall were also measured in the beginning and the end of the study. Differences in height for seedlings of selected species were examined using a 2 x 2 ANOVA, where disturbance and geologic formation (karst or volcanic) were the main effects. In most instances for both adults and seedlings, individual ANOVA's (i.e., per species) were not possible due to low sample sizes or the absence of a species in a treatment, or geologic formation. In such cases, I grouped data for all species and examined the generic question of differences in growth rates for adults and seedlings between treatments (disturbed or not) irrespective of geologic formation. When data met assumptions of normality (typically seedlings), I used a t-test. When that was not the case, I used the non-parametric equivalent, a Kruskal-Wallis test. Vegetative cover (i.e., ground and canopy cover) will be estimated using ocular tubes (Martin and Guepel 1993). Differences in canopy cover (%) and ground leaf-litter cover (%) were analyzed using a 2 x 2 ANOVA, where disturbance and geologic formation (karst or volcanic) were the main effects.

Morisita’s Index (Krebs 1989) was used to establish the possible similarity in species composition among plots and study sites. This index ranges from 0 (no similarity) to 1.0 (complete similarity). I arbitrarily used an index value of < 0.5 to indicate low similarity and ≥ 0.51 as similar. First, I calculated Morisita’s Index within study area-disturbance class for adult trees and seedlings/saplings established before the hurricane, and for adults and seedlings established after the hurricane to help understand the degree to which the species composition of the surrounding vegetation is reflected in germination, and how this may have been altered after the hurricane. Second, I calculated Morisita’s Index between disturbed and undisturbed plots for each age group to look for potential effects of the hurricane on diversity. All statistical tests were considered significant at $\alpha \leq 0.05$.

CHAPTER V

RESULTS

A total of 1346 adult individuals were identified in the study (from the plots and adjacent plots combined: total area sampled = 8800 m^2). Adult species richness on volcanic and karstic soils was roughly equal (46 vs. 45 species, respectively). The most common adults in karstic plots were the plantation species *Hibiscus elatus* (153 individuals), followed by the natives *Guarea guidonea* (88) *Calophylum antillanum* (67), and *Dendropanax arboreus* (57). In the volcanic plots, the exotic *Syzygium jambos* (175 individuals) was most common, followed by the natives *Guarea guidonia* (132), *Ocotea leucoxylon* (122), and *Casearia arborea* (56). Vertical cover was significantly greater in undisturbed sites (87%) than in disturbed ones (56%) (F = 18.75, df = 3, 156, P = 0.001). Conversely, leaf litter cover was lower in disturbed sites (24%) than in undisturbed sites (56%) (F = 8.62, df = 3, 76, $P < 0.001$).

Across all plots, 2985 seedlings and saplings from 70 woody species were tagged (total area sampled = 800 m^2). Species richness of seedlings was higher on karstic than on volcanic soils (59 vs. 37 species, respectively). Plots on volcanic soils contained four exotic species as compared to two on karstic soil plots. The native *Guarea guidonea* was the dominant species in the two karstic soil study sites and the volcanic soil Tres Picachos site, whereas the exotic *Syzygium jambos* was the dominant species in the volcanic soil Cialitos site. *Guarea guidonea* was the most common species among seedlings overall (506 individuals), followed by *Inga vera* (235) and *Ocotea leucoxylon* (64; Table 1).

The disturbed Cialitos plot had the highest number of seedlings (889 individuals). Conversely, the undisturbed Rio Abajo plot had the lowest number (145 individuals). The number of seedlings was higher in plots on volcanic soils, with 2059 (69%) in volcanic soil sites as compared to 926 (31%) in karstic soil sites. Of the 16 species used by avian species, 14 were detected across most plots, with the exception of *Inga laurina* and *Casearia guianensis* (Table 2). Of the 16 species of high use value for resident avian frugivores, seedlings of *Guarea guidonea* were most common, occurring in 67 of 80 quadrants (84%) throughout the study areas. Seedlings of an additional six species were present in more than 10 % of the quadrants; *Ocotea leucoxylon* in 29 (36.2 %), *Ocotea floribunda* in 16 (20 %), *Schefflera morototoni* in 13 (16.2 %), *Cecropia schreberiana* in 13 (16.2 %), *Inga vera* in 12 (15 %), and *Cordia sulcata* in 11 (14 %; see Table 2). Appendix I summarizes information on the general ecology of these species, with additional observations on their abundance and distribution in my study plots.

A total of 279 new seedlings from 40 species emerged during the study. More individuals germinated in the volcanic than karstic plots (151 vs 128), and in disturbed than undisturbed plots overall (149 vs. 130), as well as within each site (Tables 3 and 4). However, germination among the sites was quite variable, with particularly low germination in both Rio Abajo plots, and high germination in the undisturbed Tres Picachos and disturbed Frontón sites (Table 4). Also, species richness of new seedlings (germinated) was higher in disturbed than undisturbed plots (overall 31 species vs 20), except in the case of Tres Picachos (Table 4).

Species composition among disturbed and undisturbed plots ranged from highly similar (Moristia's index value of 0.91) to highly dissimilar (Morisita's index value of 0.02) depending on site and whether the comparison was among adults, established seedling plants, or new post-hurricane seedlings (Table 5A). Disturbed and undisturbed plots had highly similar species composition for adults only in Tres Picachos and Frontón, and for established seedlings and new seedlings (post-hurricane) at Cialitos (Table 5A). Adults and new seedlings (post-hurricane) were generally very similar in all plots, except Frontón (Table 5B).

Survival of seedlings was variable among species (Tables 6 and 7). For those species with enough data for more rigorous analyses, results follow the same pattern. Seedlings of *Alchornea latifolia* had significantly higher survival in disturbed karst study sites ($Z = 162$; $P < 0.05$; Table 8). For *Guarea guidonea*, seedlings had significantly higher survival rates in undisturbed, volcanic study sites ($Z = 3.05$, $P < 0.05$) and in disturbed, karstic study sites ($Z = 3.60$, $P < 0.05$). Survival of seedlings of *Ocotea leucoxylon* and *Syzygium jambos* did not differed between disturbed and undisturbed volcanic study sites. Adult survival was extremely high, and did not differ between disturbed and undisturbed plots (total mortality was only 1 vs. 3 individuals, respectively).

Growth in height (cm) by treatment (disturbed/undisturbed) and formation (karst or volcanic) for the seedlings of four woody species with sufficient data for rigorous analyses (i.e., ANOVA) are presented in Table 9. *Guarea guidonea* ($F = 7.48$, df = 3, 283, $P = 0.001$) and *Alchornea latifolia* ($F = 5.62$, df = 3, 124, $P = 0.001$) grew significantly faster in disturbed sites regardless of formation. Significant differences in growth were also recorded for *Syzygium jambos* (Chi-square = 47.03, df = 1, $P = 0.001$). This species was detected only in volcanic soil study plots. The average increase in basal diameter ($t = 4.52$, df = 588, $P = 0.001$) and height ($t = 5.29$, df = 2696, $P = 0.0001$) of seedlings for all species combined was significantly greater in disturbed sites (Table 10).

Only two species of trees had at least three adults in more than a single site to allow a comparison of growth rates in disturbed and undisturbed plots. Growth in height for *Guarea guidonia* (1.42 ± 1.17 SD vs. 0.65 ± 1.05; Chi-square = 4.92, P = 0.025) and *Ocotea leucoxylon* (0.90 ± 0.60 SD vs. 0.24 ± 0.19; Chi-square = 10.53, df = 1, P = 0.001) was faster in disturbed than undisturbed plots. Similarly, DBH increased faster in disturbed plots for *Guarea guidonia* (0.45 ± 0.30 SD vs. 0.24 ± 0.29; Chi-square = 4.23, df = 1, P = 0.04), and nearly so for *Ocotea leucoxylon* (0.76 ± 1.24 SD vs. 0.16 ± 0.23; Chi-square = 3.71, df = 1, P = 0.05). Interestingly, smaller individuals of *Guarea guidonia* grew faster than larger ones in disturbed plots, but size did not correlate with growth rate for undisturbed plots (Figure 2). The average increase in DBH (t = 1.91, df = 166, P 0.05) and tree height (t = 3.15, df = 166, P 0.002) for all species combined was significantly greater in disturbed than in undisturbed sites (Table 10).

CHAPTER VI

DISCUSSION

Although this study began five months after Hurricane Georges made landfall on Puerto Rico, differences in recovery patterns among the study sites were readily noticeable. The plots located in volcanic areas (Tres Picachos and Cialitos) showed signs of recovery; the canopy was closing more rapidly. The damage observed in the karstic plots was noticeably greater than in the volcanics plots. Damage consisted not only of defoliation but also breakage, uprooting, snaping, loosening and shredding of bark. This damage facilitated the establishment of vines, which could interfere with the re-establishment of the forest for years. Differences in damage between karstic and volcanic study sites might help explain some of the differences reported in this study, although other factors are discussed below.

In general, damage to forest structure was reflected by a significantly lower canopy cover in disturbed sites. Leaf litter cover, however, was not greater in disturbed sites despite the apparent damage to vegetation structure. The patchy nature of leaf litter cover in disturbed sites could have been the result of wind. Unfortunately, I did not measure litter depth, a factor that could have affected germination (Guzman–Grajales and Walker 1991, Lodge et al. 1991).

This study demonstrated that germination of all plant species, including the 16 of special interest, was possible across all study plots, including undisturbed plots in Rio Abajo and Frontón, where the closed canopy made it more difficult due to poor light penetration. Consistently, the density of seedlings of many species was higher in disturbed sites, although much of this difference was established prior to the hurricane.

During this study, 279 new seedlings germinated, or 9.36 % of the total individuals that grew in the eight study plots (2,981). Both the total number of individuals that germinated, and the species richness of those new recruits was higher in the disturbed plots. Generally, the species composition of seedlings reflected that of the adults in the immediate vicinity, yet the difference in species richness among new seedlings (post-hurricane) was higher than that among adults, suggesting that disturbed conditions were favorable to a broader array of species than undisturbed conditions. By and large, my results lend support to the initial floristic hypothesis (Engler 1954).

The high number of seedlings and saplings of some species in various plots was probably aided by source of seeds from existing parental trees. This was probably the case for *Guarea guidonea* in Tres Picachos, *Syzigium jambos* in Cialitos, and *Hibiscus elatus* in the undisturbed study site of Rio Abajo. Observations in support of my contention come from branches of *Guarea guidonea* found on the floor with dried fruits in intermediate stage of development. This suggested to me that when the hurricane hit, *Guearea* was in reproductive stage. The seeds from those fruits likely had the best opportunity to germinate. For all species, the increase in germination occurred in the first period of measurement (Table 3), five months after the passage of hurricane Georges.

Species composition was consistently different among the disturbed and undisturbed plots except in adults in Tres Picachos and Fronton, and for seedlings and new recruits (germination) in Cialitos. Clearly, these differences were established ones (prior to the hurricane) and generally not affected by the hurricane. However, a higher number of different species were established in disturbed than undisturbed plots throughout the study sites with the exception of the undisturbed plot in Tres Pichachos.

Growth in some species was greatly enhanced by the disturbance of Hurricane Georges. The only two tree species had large enough samples to compare *Guarea guidonia* and *Ocotea leucoxylon* grew significantly more in disturbed sites. Moreover, small *Guarea guidonia* grew proportionally more in than larger individuals in disturbed plots and than small ones in undisturbed plots, suggesting that smaller individuals are suppressed in closed canopy, and that disturbance may be particularly important for success of this species. Seedlings of *Guarea guidonia* and *Alchornea latifolia* grew faster in the disturbed sites. The benefits of disturbance were also surmised when data for seedlings and adults of all species were examined together. For both height and basal diameter, growth rates were significantly higher in disturbed sites. This was not the case for trees despite the differences in canopy cover between treatments (disturbed or not), a reflection of hurricane damage on that layer. It is possible that recovery (e.g., leafing) occurred quickly enough to make differences in growth rates indistinguishable. The production of new leaves is generally rapid in some tree species. Walker and Neris (1991) reported new leaves within two weeks after Hurricane Hugo in the Luquillo Experimental Forest. Sprouting of new branches appeared within seven weeks and was more common on snapped than uprooted stems or on stems without major damage (Walker 1991). In this study, sprouting of new branches was common in the teca plantation (*Tectona grandis*) plot on Rio Abajo Forest.

Survival of *Guarea guidonea* seedlings, at least in karstic study sites, was higher in disturbed plots as compared to undisturbed ones. Seedling survival appeared to be fairly high in this study (81-95%). Steven (1994) report similar results for *Tetragastris panamensis* for the first year in a long-term study in Barro Colorado Island. These findings suggest that the disturbance caused by the hurricane was not only an important agent for increasing germination, but also to foster higher survival among new seedlings. It is likely that gaps created by hurricane Hugo also promoted an increase in recruitment of plants from one size class to another through enhanced survival and growth (Figure 2, Brokaw & Grear 1991, Fernández & Fletcher 1991).

Several factors could have affected germination in this study. One of them was litterfall from *Cecropia schreberiana* and *Hibiscus elatus.* Consistent with my results on percent cover of leaf-litter, some undisturbed plots in the study site Tres Picachos were noticibly impacted by large *Cecropia* leaves covering the ground (leaves can reach 30-50 cm in diameter). These leaves may not have caused the death of seedlings, but likely reduced the number of seedlings that could germinate by blocking sunlight (Bruederle and Stearns 1985, Guzman-Grajales and Walker 1991, Lodge et al. 1991). The quantity of litterfall produced by *H. elatus* and the closed canopy of these plantation forests probably also had a direct effect over germination and mortality of the seedlings. In tropical forests, local canopy structure strongly affects the growth of saplings (Clark and Clark 1987).

Another factor that may have influenced seedling survival and growth was low levels of rainfall during my study. Precipitation data collected by NOAA at the Dos Bocas Station (near the Rio Abajo study plot, and within the same karstic region that includes Frontón) indicates that the total rainfall for July 1999 was 28.9 mm, well below the 71.2 mm long-term annual average and lowest for all months in 1999. Many seedlings that germinated over the litterfall died during this period of lower rainfall, with species such as *Eugenia monticola* and *Guarea guidonea* being most affected. From my observations, I also suspect that fungi affected germination and survival, especially of Sy*zigium jambos* seedlings.

This study has shown that the creation of gaps facilitates germination, influences survival and growth, and can possibly lead to the replacement of plant species that were inhibited from growing by the species comprising the canopy cover prior to the disturbance. The number of plant species that germinated in my study plots highlight the role played by neighboring parental trees, but also the potential role of the seed bank and seed dispersal. Poor relationship between plot seedling species composition and neighboring adult trees (e.g., Fronton) exemplifies that possibility. Clearly, creating gaps in natural or managed forests (e.g., Rio Abajo) could be a powerful tool to promote the presence of native plant species. In the specific case of avian conservation, this tool can be used to promote native plant species regeneration, which will likely include some fo the 16 species of special interest in this study, and subsequently, promote the presence and resource use by avian species (e.g., Carlo et al. In Press).

CONCLUSIONS

1. The species composition was different between disturbed and undisturbed plots.
2. The Hurricane Georges increased the recruitment of the seedlings.
3. The changes in canopy structure caused by Hurricane Georges increased the growth of the seedlings (e.g.; the specie *Guarea guidonea* grew significantly in disturbed sites)
4. The height and diameter of seedlings and adults of alls species were significantly higher in disturbed plots.
5. At least 14 of 16 species of interest germinated across the study plots.

RECOMMENDATIONS

1. Establish experimental plots in selected forest reserves of Puerto Rico to monitor long term species recruitment and growth. Selected reserves should represent the range of conditions and potential for management found in the forest reserves systems of PRDNER.
2. Establish experimental plots in selected forest reserves of Puerto Rico immediately after a hurricane strikes the Island to monitor the long term effect of these atmospheric events on seedlings germination rate and recruitment.
3. Implement management practices aimed at increasing recruitment of species of interest in selected plots (e.g.; gap creation, thinning, fertilizer, weeding).

LITERATURE CITED

Acevedo Gilberto. 1982. Soil survey of Arecibo of Northern Puerto Rico. United State, Department of Agriculture Soil Conservation Service in Cooperation with the College of Agriculture, University of Puerto Rico, Mayagüez Campus. 182 pp.

Acevedo, Rodriguez P, Axelrod Franklin 1999. Annotated Cheklist for the Tracheophytes of Rio Abajo Forest Reserve, Puerto Rico. Caribbean Journal of Science, Vol., 35, No. 3-4, 265-285.

Birdsey, Richard A., Weaver, Peter L. 1982. The forest resources of the Puerto Rico. Res. Bull. SO- 85. New Orleans LA:U.S. Department of Agriculture, Forest Services, Southern Forest Experiment Station. 59 pp.

Brokaw, N. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. J. Ecol. 75: 9-20.

Brokaw, N.V.L. and Walker, R.L. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23: 442-447

Brokaw, N.V.L. and Grear, J.S. 1991. Forest structure before and after hurricane Hugo at three elevations in the Luquillo mountains, Puerto Rico. Biotropica 23: 386-392

Browndarle, L. P., and F. W. Sterns. 1985. Ice storms damage to a southern Wisconsin mesic Forest. Bull. Torrey Bot. Club 112: 167-175.

Butler, B. J. and Chazdon, R.L. 1998. Species richness spatial variation, and abundance of the soil seed bank of a secundary tropical rain forest. Biotropica 30(2): 214-222

Cardona, J. E., Rivera M., Laboy, C. y Vázquez, M. 1985. La posible reintroducción de la cotorra puertorriquena (Amazona vittata) al Bosque de Rio Abajo: una evaluación de la disponivilidad de cavidades para su anidamiento. Duodécimo Simposio De Recursos Naturales. 308-328.

Cardona, J.E., M. Rivera, M. Vazquez-Otero and C.R. Laboy. 1986. Availability of food resources for the Puerto Rican parrot and the Puerto Rican plain pigeon in Rio Abajo Forest. Puerto Rico Dept. of Natural Resources, Draft Project Report No. W-10 (ES-1).

Carlo,T.A. 1999. Diet, fruit preference and seed dispersal capabilities of fruit-eating birds in north central Puerto Rico. M.S. Thesis. North Carolina State University. 107 pp.

Carlo, T.A., J.A. Collazo and M.J. Groom. 2003. Avian fruit preference and seed dispersal effectiveness: A view of landscape variation of bird-plant interactions. Oecologia 134:119-131.

Carlo, T.A., J.A. Collazo and M.J. Groom. In Press. Avian Foraging in Shaded Coffee Plantations: Influence of Fruit Abundance, Plant Species Composition, and Conservation Implications. Biotropica.

Carlton, G.C., and F. A. Bazzaz. 1998. Regeneration of tree sympatric birch species on experimental hurricane blowdawn microsites. Ecology Monogr. 68: 99-120.

Chazdon, R.L. 1988. Snuffles and their importance to forest understory plants. Adv. Ecol. Res. 18: 1-63.

Cheke, A.S., W. Nanakorn, and C.Ynakoses. 1979. Dormancy and dispersal of seed of secundary forest species under the canopy of a primary tropical rainforest in northern Thailand. Biotropica 11: 88-95

Chinea, J.D., 1980. The forest vegetation of the limestone hills of northern Puerto Rico. Cornell University, Master thesis.

Clark, D.A.; and D.B. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent. Biotropica 19: 236 –244

Clark, D.B., and D.A. Clack. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest, Oikos 55: 225 – 230.

Collazo, J. A., T. H. White, F. J. Vilella, and S. Guerrero. 2003. Survival of captive-reared Hispaniolan Parrots released in Parque Nacional del Este, Dominican Republic. Condor 105: 198-207.

Collazo, J.A. and M.J. Groom. 2000. Avian conservation in north-central forested habitats in Puerto Rico. Final report, Puerto Rico Dept. of Natural and Environmental Resources, Federal Aid Project W-20, San Juan, PR. 245 pp.

Dalling, J.W., M.D.Swaine and N.C.Garwood. 1997. Soil seed bank community dynamics in seasonally mist lowland tropical forest, Panama. J. Trop. Ecol. 13: 659-680.

Dalling, J.W., M.D.Swaine and N.C.Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79: 564- 578.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Ann. Rev. Ecol. Syst. 1987. 18: 431-451

Doak, D.F. and W. Morris. 1999. Detecting population-level consequences of ongoing environmental change without long- term monitoring. Ecology 80:1537-1551.

Engler, F.E. 1954. Vegetation Science Concepts 1. Initial floristics composition in old vegetation development. Vegetatio 4: 412-417.

Ewel; G. G. and G. L. Whitmore. 1973. The Ecological life zone of Puerto Rico and the U.S. Virgin Islands. U.S.D.A. For. Serv. Res. Pap. ITF-18. 72 p. Inst. Trop. For.; Rio Piedras, P.R.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, London, England.

Fernandez, D.S. and Fetcher, N. 1991. Changes in light availability following hurricanes Hugo in a subtropical montane forest in Puerto Rico. Biotropica 23 (4a): 393-399.

Field, C.B. and Vázquez, Y.C. 1993. Species of the genus Piper Provide a model to study how plants can grow in different kinds of rain forest habitats. Interciencia, vol.18, No 5: 230-236.

Foster, S.A. 1987. On the adaptive value of large seeds for tropical moist forest trees: A review and synthesis. Bot. Rev. 52: 260-99.

Francis, K. John. 1994. *Inga fagifolia* (L.) Willd. Guama SO-ITF-SM-72 :1-4 pp.

Francis, J. K. and Lowe; C.A. 2000. Silvics of Native and Exotics Tree of Puerto Rico and the Caribbean Islands. U.S.D.A. International Institute of Tropical Forestry Rio Piedras P.R. 582 p.

Francis; J.K.; Rodriguez, A. 1973. Seeds of Puerto Rican trees and shrubs: Second installment. Res. Note.SO- 374. New Orleans, L A.: U.S. Department of Agriculture, Forest Services, Southern Forest Experimental Station. 5 p.

Gleason, H. A. and Cook, M.T. 1927. Scientific Survey of Porto Rico and the Virgin Islands. Vol.VII- Part 1 New York Academics of Science.

Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. J. Ecol. 78: 1079-1093.

Guevara, S., and A. Gómez-Pompa. 1976. Determinación del contenido de semillas de muestras de suelo superficial de una selva tropical de Veracruz, mexico. In A. Gómez-Pompa, C. Vázquez-Yanes, S. Del Amo, and A.Butanda, (Eds.). Investigaciones sobre la regeneración de selvas altas en Veracruz, Mexico, pp. 203-232. Compañía Editorial Continental, Mexico City, Mexico.

Guzman, G.S.M. and Walker, L.R. 1991. Differential seedling responses to litter after Hurricanes Hugo in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 407-413.

Herwitz, S.R. 1981. Regeneration os selected tropical tree species in ConcovadoNational Park, Costa Rica. University of California Publications in Geography. 24: 1-109.

Howe, H.F., and G.F. Estabrook. 1977. On interspecifics competition for avian disperser in tropical trees. American Naturalist No. 111: 817 – 832.

Hopkins, M. S. and Graham, A.W. 1983. The species composition of soil seed banks beneath lowland tropical rainforest in north Queensland, Australia. Biotropica 15: 90-99.

Jenkins; Machael B. 1988. The useful trees of Haiti: a selected review.238 p. Unpublish data achived at the U.S. Department of Agriculture. International institute of tropical forestry, Rio Piedras P.R.

Jordano P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: dependence asymmetries, and coevolution. American Naturalist 129:657-677.

Jordano P., J. Bascompte, J.M. Olesen. 2003. Invariant properties in coevolutionary networks of animal-plant interactions. Ecology Letters 6:69-81.

Joung, K. R.; J. J. Ewell. and B. J. Brown. 1987. Seed dynamics during forest secession in Costa Rica. Vegetatio 71:157-173.

Krebs, Charles J. 1989. Ecological Metodology. University of British Columbia, Harper Collins Publishers.654pp.

Leck, Charles F. 1972. Observations of birds at *Cecropia* trees in Puerto Rico. The Wilson Bulletin 84:498- 500.

Leon, J. 1966. Central America and West Indian Species of Inga (Leguminosae). Annuals of Missouri BotanicalGarden 53:265-359.

Liegel, L. H. 2000. Silvics of Native and Exotics Tree of Puerto Rico and the Caribbean Islands. 582pp.

Loigier A. Henri, Martorell F. Luis. 1982. Flora of Puerto Rico and Adjacent Islands: a systematic synopsis. 342pp.

Little, E. L. Jr.; Woodbury. R. O. 1976. Trees of the Caribbean National Forest, Puerto Rico. Res. Pap. ITF-20. Rio Piedras, PR: U.S. Department of Agriculture, Forest Service, Institute of Tropical Forestry. 27pp.

Little. E. L.; Jr; Wadsworth, F. H. 1964. Common trees of Puerto Rico and theVirgin Island. Agriculture Handb. 249 Washington Dc: U.S. Department of Agriculture. 548 p.

Little. E.L.; Jr.; Wadsworth, F.H. 1991. Common Trees of Puerto Rico and the Virgin Islands. Second Edition. U.S. Department of Agriculture, Washington, D.C.

Little, E. L. Jr.; Woodbury. R. O. and Wadsworth, F. H. 1974. Arboles de Puerto Rico y las Islas Virgenes. Segundo Vol. 1117 p.

Lodge, D.J., Scatena, F.N., Asbury, C.E. and Sanchez, M.J. 1991. Fine litterfall and related nutrient inputs resulting from Hurricanes Hugo in subtropical wet and lower montane rain forest of Puerto Rico. Biotropica 23: 336-342.

Lugo, A.E., Appletted, M., Pool, D.J. and McDonald, R.B. 1982. The impact of Hurricane David on the forest of Dominica. Canadian Journal of Forestry Research vol. 13: 201-211.

Lynch, J. F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23:488-496.

Mackey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159-191 in coevolution of animal and plants. Univ. of Texas Press. Asting, Texas USA.

Marrero, J. 1948. Forester planting in the Caribbean National Forest: past experiences as a guide for the future. Caribbean Forester 9: 85-146.

Marrero; J. 1949. Tree seed data from Puerto Rico. Caribbean forester 10: 11-30.

Marrero, J. 1950. Results of forest planting in the insular forest of Puerto Rico. Caribbean Forester. 11: 107-147.

Marshall, R.C. 1939. Silviculture of the Trees of Trinidad and Tobago, British. West Indies. London: Oxford University Press 247p.

Martin, T. E. and G. R. Geupel. 1993. Protocols for nest monitoring: Locating nests, monitoring success and measuring vegetation. J. Field Ornith. 64:510-519.

Mckenzie, P.M., Noble, R.E. 1989. Notes of a large foraging concentration of endangered Yellow-Shouldered Blackbird (*Angelaius xanthomus*) in southwestern Puerto Rico. Caribbean Journal of Science. Vol. 25 No.1-2

Morrison, M.L B.G. Margot, and R. W.Mannan. 1998. Wildlife-habitat relation concepts and applications. 2 nd. edition. The University of Wisconsin Press, Madison, Wisconsin 458 pp.

Nieves, L.O. 1979. Ecological life history study of *Didymopanax morototoni*: Ro Piedras; P.R: University of Puerto Rico. 85 Tesis de M.S.

Pascarella, J.B. 1998. Hurricane disturbance Plant –Animal interactions, and reproductive success of a tropical schrub. Biotropica 30: 416-424

Perez-Rivera , R.A. 1991. Change in diet and foraging behavior of the Antillean euphonia in Puerto Rico after hurricane Hugo. J. Field Ornithol. 62: 474-478.

Perez- Rivera, R.A. 1994. Feeding ecology of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in the Carite and Guánica Forest. Carib. J. Sci. 30: 242-249.

Pickett. S. T.A. and White, P.S. eds. 1985. The ecology of natural disturbance and patch dynamics. New York: Academics press, 472 pp.

Peterson; C.J.; and S.T.A. Pickett. 1990. Microsite and elevation influences on early forest regeneration after catastrophic windthrow. J. Veg. Sci.1: 657-662.

Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D.Curtis. 1989. Survival analysis in Telemetry studies: the stagger entry design. J. Wild. Manage 53: 7-15.

Pompa, J, and Bongers, F. (1988). The effect of canopy gaps on growth and morphology of rain forest species. Oecologia 75: 625-632.

Putz; F. E. 1983. Treefall pits and mounts, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island. Panama. Ecology 64: 1069-1074.

Rivera, L.W. and Aide, T.M. 1997. Forest recovery in the karst region of Puerto Rico. Forest Ecology and Management 108. 63-75.

Sandford, R.L., Jr., W.J. Parton, D.S. Ojima, and D.L. Lodge. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: result for simulation modeling. Biotropica 23: 364-372.

Saracco, J. F. 2001. Fruit neighborhoods, and birds and plants interactions in north central Puerto Rico. Ph.D. Dissertation, North Carolina State University. 180 pp.

Saracco, J.F., J.A. Collazo, M.J. Groom, and T.A. Carlo. In Press. Crop Size and Fruit Neighborhood Effects on Bird Visitation to Fruiting *Schefflera morototoni* Trees in Puerto Rico. Biotropica.

Saracco, J.F., J.A. Collazo, and M.J. Groom. 2004. How do frugivores track resources? insights from spatial analyses of birds foraging in a Puerto Rican forest. Oecologia 139:231-245.

Silander, Susan R. 1979. A study of ecological life history of *Cecropia peltata* L.; an early secondary sucessional species in the rain forest of Puerto Rico. Knoxville, TN. University of Tenessee. 94 p. Thesis M.S.

Smith, R. F. 1970. The vegetation structure of a Puerto Rican rain forest and after short-term gamma radiation. En: Odum, H.T.; Pigeon, R. F.; eds. A tropical rain forest. Springfield, VA: U.S.Department of Commerce: 103-140. Capitulo D-3.

Snow, D. 1970. Evolutionary aspects of fruit eating in birds. Ibis No. 113:194-192

Snyder, N.F.R., J.W. Wiley and C.B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican parrot. West. Found. Vertebr. Zool., Los Angeles, CA. 384 pp.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecological System: 15: 353-391.

Steavens, D.D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consecuences for tree canopy species in Panama. Journal of tropical Ecology 10: 369-383.

Steudler, P.A., J.M. Melillo, R.D. Bowden, M.S. Castro, and A.E.Lugo. 1991. The effects of Natural and human disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. Biotropica 23: 356-363.

Swaine, M.D., and J.B.Hall. 1983. Early succession on cleared forest land in Ghana. J. Ecol. 75: 601- 627.

Swaine, M. D.; T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forest in Costa Rica. Vegetatio 75: 81- 86.

Tanner, E.V.J., Kapos V. and Healy, J.R. 1991. Hurricanes effects on forest ecosystems in the Caribbean. Biotropica 23 (4a): 513-521.

Taylor, B.W. 1963. An Outline of the Vegetation of Nicaragua. Journal of Ecology. 51: 27-54.

Thomson, K. 1992. The funtional ecology of seed bank. In M. Fenner 9Ed.). Seeds: the ecology of regeneration in plant communities. C.A.B. International, United Kingdom.

U.S. Fish and Wildlife Service. 1999. Technical/Agency Draft Resvised Recovery Plan for the Puerto Rican Parrot (*Amazona vittata*). Atlanta, Georgia. 77pp.

Vazquez- Yanes. C., E. Rincon, M. E. Sanchez – Coronado, P. Huante, J.R. Toledo, and V. L. Barradas. 1990. Light beneath the litter in a tropical forest: effect on seed germination. Ecology 71: 1952- 1958.

Vitousek; P.M. 1984. Litterfall nutrients cycling, and nutrients limitation in tropical forest. Ecology 65: 285-298.

Wadsworth, F. H. 1950. Notes on the climax forest of Puerto Rico and their distribution and conservation prior to 1900. Caribbean Forester 11 (1): 38-47.

Wadsworth, F.H., and Englerth, G.H. 1959. Effects of the Hurricanes Betsy on forest of in Puerto Rico. Caribbean Forester Vol. 20 nos.1 and 2.

Waide, R. B. 1991. Summary of response of animal population to hurricanes in the Caribbean. Biotropica 23:508-512.

Walker, L.R. and Neris, L.E. 1993. Posthurricane seed rain dynamics in Puerto Rico. Biotropica 25: 408-418.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest of Puerto Rico. Biotropica 23: 379-385.

Weaver, L. Peter. 1988. *Guarea guidonea* (L.) Sleumer American mushwood SO-ITF-SM-17 1-7 pp.

Weaver, P.L. 1986. Hurricane damage and recovery in the montane forest of the Luquillo mountains of Puerto Rico. Caribbean Journal of Science 22: 53-70.

Weaver, P.L. 1986. Forest changes after hurricane in Puerto Rico Luquillo Mountains. Interciencia 44:181-192.

Weaver, P.L. 2000. Silvics of Native and Exotic Trees of Puerto Rico and the Carebbean Island 582 p.

Wetmore, A. 1916. Birds of Porto Rico. USDA Bulletin 326. Washington, D.C.

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study Supplement 46: 120-138.

Whitmore, T.C. 1975. Tropical rain forest of the east. Claredon Press, Oxford, England.

Wiley, J.W. and Wunderle, J.M. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Birds Conservation International 3:319-349.

Wunderle, J. M. 1999. Pre-and Post-hurricane fruit availability: implications for Puerto Ricans Parrots in the luquillo Mountains. Carib. J. Sci. 35: 249-264.

You, C.; and W. H. Petty. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree speciesws in the Luquillo Experimental Forest of Puerto Rico. Biotropica 23: 400- 406.

Young. K. R., J. J. Ewell. And B. J. Brown 1987. Seed dynamics during forest succession in Costa Rica. Vegetatio 71: 157-173

Zar, J. H. 1996. Biostatistical Analysis. 3rd edition. Prentice Hall, Inc., NJ.

Zimmerman, J. K., Aide; T.M., Rosario, M., Serrano, M., Herrera, L., 1995. Effects of land Management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 77: 65-76.

Zimmerman, J. K., Everham III. E. M., Waide, R. B., Lodge, D.J., Taylor, C. M., Brokaw, N. V. L. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life history. J. Ecol. 82: 911-922.

Table 1. The total number of seedlings and saplings, mean density and relative density of 16 species of interest in montane and karstic forests in north-central Puerto Rico (all 8 study plots combined).

Species	Family	Total num.	Mean density	Relative density%
Volcanic				
Guarea guidonea	Meliaceae	374	9.35	18.16
Inga vera	Mimosoideae	170	4.25	8.26
Ocotea leucoxylon	Lauraceae	58	1.45	2.81
Scheflera morototoni	Araliaceae	57	1.43	2.77
Cordia sulcata	Boraginaceae	23	0.57	1.11
Cecropia shcreberiana	Moraceae	7	0.17	0.33
Miconia prasina	Melastomataceae	8	0.20	0.39
Miconia serrulata	Melastomataceae	4	0.10	0.20
Ocotea floribuna	Lauraceae	2	0.05	0.09
Andira inermis	Papilionaceae	1	0.02	0.04
Casearia arborea	Flacourtiaceae	1	0.02	0.04
Casearia sylvestris	Flacortiaceae	0	0	0
Inga laurina	Mimosoideae	0	0	0
Clusia rosea	Clusiaceae	0	0	0
Casearia guianensis	Flacourtiaceae	0	0	0
Casearia decandra	Flacourtiaceae	0	0	0
Karstic				
Guarea guidonea	Meliaceae	132	3.30	14.25
Inga vera	Mimosoideae	65	1.62	7.38
Cecropia shreberiana	Moraceae	41	1.02	4.45
Ocotea floribunda	Lauraceae	20	0.5	2.17
Andira inermis	Papilionoideae	7	0.17	0.76
Ocotea leucoxylon	Lauraceae	6	0.15	0.65
Miconia prasina	Melastomataceae	5	0.12	0.54
Scheflera morototoni	Araliaceae	4	0.1	0.43
Casearia decandra	Flacourtiaceae	4	0.1	0.43
Schefflera morototoni	Araliaceae	4	0.1	0.43
Casearia sylvestris	Flacourtiaceae	3	0.07	0.32
Cordia sulcata	Boraginaceae	3	0.07	0.32
Clusia rosea	Clusiaceae	1	0.02	0.25
Miconia serrulata	Melastomataceae	0	0	0
Casearia arborea	Flacourtiaceae	0	0	0
Casearia guianensis	Flacourtiaceae	0	0	0
Inga laurina	Mimosoideae	0	0	0

Total number of individuals for Montane Forest = 2059; total number of individuals for Karstic Forest = 921.

Table 2. Frequency of occurrence (% of 80 quadrats occupied) of seedlings and saplings of 16 species of interest in all 8 study plots in north- central Puerto Rico.

Species	**Num.of quadrats**	**Frecuency of occurrence (%)**
Guarea guidonea	67	84.0
Ocotea leucoxylon	29	36.2
Ocotea floribunda	16	20.0
Cecropia schreberiana	16	20.0
Schefflera morototoni	14	17.5
Inga vera	12	15.0
Cordia sulcata	11	14.0
Miconia prasina	6	7.5
Casearia arborea	6	7.5
Miconia serrulata	5	6.2
Andira inermis	5	6.2
Casearia silvestris	3	4.0
Casearia decandra	1	1.2
Clusia rosea	1	1.2
Inga laurina	0	0
Casearia guianensis	0	0

Table 3. Seedlings that germinated during the study in disturbed vs. undisturbed plots in 8 study plots in north- central Puerto Rico.

Species	**Disturbed**	**Undisturbed**
Alchornea latifolia	4	4
Amiris elemifera	2	0
Ardisia obovata	1	0
Buchenavia capitata	1	0
Calophylum antillanum	0	1
Casearia arborea	0	1
Cecropia schreberiana	1	0
Cinnamomun elongatum	5	0
Cinnamomun montanum	1	0
Cordia sulcata	1	0
Dendropanax arboreus	0	1
Eugenia monticola	20	2
Ficus mammifera	2	0
Guarea guidonea	30	60
Inga vera	6	0
Lepianthes peltata	0	2
Miconia serrulata	2	1
Miconia sp.	0	1
Ochroma lagopus	1	0
Ocotea floribunda	0	3
Ocotea leucoxylon	1	5
Picramnia pentandra	3	0
Pimenta racemosa var grisea	2	0
Piper aduncum	2	3
Piper amalago	1	0
Piper glabrescens	1	1
Piper marginatum	1	0
Psychotria berteroana	7	5
Psychotria pubescens	1	0
Roystonea borinquena	0	2
Sapium laurocerasus	2	0
Schefflera morototoni	3	0
Sideroxylum foetidissimun	0	1
Solanum erianthum	2	0
Spondias mombin	3	0

Table 3. Continued

Syzigium jambos	16	14
Thouinia striata var striata	10	14
Trichilia pallida	1	14
Zanthoxylum martinicense	3	1
Unknown	5	0
Total New Seedlings	**149**	**130**
Total of Established Plants in Plots	**2009**	**972**

Table 4. Species richness and total number of new seedlings that emerged in each study plot during the study in north-central Puerto Rico.

Study Area	**Volcanic**		**Karst**	
	D	**U**	**D**	**U**
Cialitos	8/33	6/18	0	0
Tres Picachos	8/33	10/67	0	0
Frontón	0	0	17/71	11/39
Rio Abajo	0	0	8/12	3/6

Table 5. Similarity of species composition between disturbed and undisturbed plots at each study site in north-central Puerto Rico. A. Comparison of species composition (Morisita's index) in disturbed and undisturbed plots among adults, seedlings (pre-hurricane), and seedlings (post-hurricane). B. Comparison of species composition (Morisita's index) between adults and post-hurricane seedlings in the plots. (0) no comparison as there were no seedlings.

A.

Study Area	**Adults**	**Seedlings (pre-hurricane)**	**Seedlings (post-hurricane)**
Cialitos	0.19	0.91	0.72
Tres Picachos	0.62	0.37	0.51
Frontón	0.62	0.21	0.28
Rio Abajo	0.02	0.11	0.41

B.

Study Area	**Volcanic**		**Karstic**	
	D	**U**	**D**	**U**
Cialitos	0.85	0.66	0	0
Tres Picachos	0.73	0.77	0	0
Frontón	0	0	0.47	0.15
Rio Abajo	0	0	0.76	0.54

Table 6. Numbers of seedlings (<10 cm in height) observed at each census period in montane and karstic forest sites for all study plots combined in north-central Puerto Rico. Censuses were conduted from February 1999 (period 1) to January 2000 (period 3). # Period = number of seedlings found at each census period. Sur. = total number of seedlings that survived over the study, Mor.= total number of seedlings that died during the study.

	VOLCANIC						**KARSTIC**					
Species	**# Period**			**Mean density**	**Sur.**	**Mor.**	**# Period**			**Mean density**	**Sur.**	**Mor.**
	1	**2**	**3**				**1**	**2**	**3**			
Guarea guidonea	43	27	33	2.57	80	23	23	8	6	0.92	31	6
Inga vera	4	6	0	0.5	11	9	1	0	0	0.02	0	1
Alchornea latifolia	17	1	1	0.47	8	11	6	0	0	0.15	1	5
Lepianthes peltata	1	0	0	0.02	1	0	1	2	0	0.07	3	0
Miconia serrulata	2	1	2	0.12	3	2	0	0	0	0	0	0
Ocotea leucoxylon	6	2	2	0.25	10	0	0	0	0	0	0	0
Piper glabrescens	9	1	0	0.25	5	5	0	0	0	0	0	0
Coffea arabica	13	2	0	0.37	15	0	0	0	0	0	0	0
Buchenavia tetraphylla	7	1	0	0.2	8	0	0	0	0	0	0	0
Psychotria berteroana	27	6	1	0.85	14	20	0	0	0	0	0	0
Syzygium jambos	161	2	1	4.1	131	33	0	0	0	0	0	0
Myrsine coriacea	1	0	0	0.02	1	0	0	0	0	0	0	0
Prestoea montana	1	0	0	0.02	1	0	0	0	0	0	0	0
Myrcia splendens	1	0	0	0.02	1	0	0	0	0	0	0	0
Schefflera morototoni	46	0	1	1.17	13	33	1	0	0	0.02	1	0
Solanum rugosum	9	0	0	0.22	4	5	2	0	0	0.05	1	1

Table 6. (Continued)

Cordia sulcata	4	1	0	0.12	0	5	2	0	0	0.05	1	1
Byrsonima spicata	1	0	0	0.02	1	0	0	0	0	0	0	0
Zanthoxylum martinicense	1	0	0	0.02	0	1	9	3	1	0.32	8	5
Piper hispidium	1	0	0	0.02	0	1	0	0	0	0	0	0
Cinnamomun elongatum	1	0	0	0.02	1	0	0	0	0	0	0	0
Cordia alliodora	1	0	0	0.02	1	0	0	0	0	0	0	0
Piper adumcum	0	0	0	0	0	0	22	5	0	0.67	21	6
Piper marginatum	0	0	0	0	0	0	3	1	0	0.1	4	0
Cecropia schreberiana	0	0	0	0	0	0	22	0	0	0.55	7	15
Piper amalago	0	0	0	0	0	0	1	1	0	0.05	2	0
Eugenia monticola	0	0	0	0	0	0	84	13	7	2.6	100	4
Spathodea campanulata	0	0	0	0	0	0	3	0	0	0.07	2	1
Ochroma lagopus	0	0	0	0	0	0	0	1	0	0.02	1	1
Thouinia striata	0	0	0	0	0	0	3	20	4	0.67	18	9
Psychotria pubescens	0	0	0	0	0	0	0	1	0	0.02	1	0
Eugenia confusa	0	0	0	0	0	0	1	0	0	0.02	1	0
Amyris elemifera	0	0	0	0	0	0	0	0	3	0.07	3	0
Solanum erianthum	0	0	0	0	0	0	0	1	0	0.02	0	1
Sapium laurocerasus	0	0	0	0	0	0	6	2	0	0.2	5	3
Pimenta racemosa var. grisea	0	0	0	0	0	0	1	0	0	0.02	1	0

Table 6. (Continued)

Ardisia obovata	0	0	0	0	0	0	2	1	0	0.07	3	0
Calophylum calaba	0	0	0	0	0	0	1	1	0	0.05	2	0
Ficus stahlii	0	0	0	0	0	0	5	2	0	0.17	4	3
Trichilia pallida	0	0	0	0	0	0	4	15	0	0.47	19	0
Spondias mombin	0	0	0	0	0	0	1	2	1	0.1	4	0
Hibiscus elatus	0	0	0	0	0	0	52	0	0	1.3	0	52
Ocotea floribunda	0	0	0	0	0	0	1	2	1	0.1	4	0
Roistonea borinquena	0	0	0	0	0	0	0	1	1	0.05	2	0
Cupania americana	0	0	0	0	0	0	2	0	0	0.05	2	0
Psychotria brachiata	0	0	0	0	0	0	1	0	0	0.02	1	0
Miconia prasina	0	0	0	0	0	0	1	0	0	0.02	1	0
Dendropanax arboreus	0	0	0	0	0	0	0	0	1	0.02	1	0
Coccothrinax alta	0	0	0	0	0	0	2	0	0	0.05	2	0
Drypetes glauca	0	0	0	0	0	0	1	0	0	0.02	1	0
Sideroxylum foetidissimum	0	0	0	0	0	0	0	1	0	0.02	1	0

Table 7. Percent survivorship (number of individuals) of seedlings and saplings of the 16 species used frequently by resident avian species in disturbed and undisturbed plots in north-central Puerto Rico. Survival is defined as number of individuals alive the beginning (February 1999) and the end of the study (January 2000).

Species	**Volcanic Disturbed**	**Volcanic Undisturbed**	**Karstic Disturbed**	**Karstic Undisturbed**
Guarea guidonea	83 % (192)	82 % (119)	77 % (69)	85 % (35)
Ocotea leucoxylon	100 % (31)	81 % (22)	100 % (4)	100 % (2)
Ocotea floribunda	100 % (2)	0 (0)	80 % (4)	100 % (15)
Cecropia schreberiana	29 % (2)	0 (0)	44 % (15)	14 % (1)
Shefflera morototoni	26 % (15)	0 (0)	100 % (3)	100 % (1)
Inga vera	77 % (131)	100 % (1)	97 % (62)	0 (0)
Cordia sulcata	62 % (8)	85 % (6)	67 % (2)	100 % (1)
Miconia prasina	0 (0)	100 % (8)	0 (0)	100 % (5)
Casearia arborea	100 % (1)	100 % (7)	0 (0)	0 (0)
Miconia serrulata	100 % (1)	66 % (2)	0(0)	0 (0)
Andira inermis	0(0)	0(0)	100 % (7)	0 (0)
Casearia decandra	0(0)	0(0)	0(0)	100 % (4)
Clusia rosea	0(0)	0(0)	0(0)	100 % (1)
Casearia silvestris	0(0)	0(0)	100 % (1)	100 % (2)
Casearia guianensis	0(0)	0(0)	0(0)	0(0)
Inga laurina	0(0)	0(0)	0(0)	0(0)

Table 8. Survival (probability of surviving from February 1999 to January 2000) of seedlings and saplings in north-central Puerto Rico in disturbed and undisturbed study sites. Significant in survival between disturbed vs. undisturbed sites within soil type (karstic or volcanic) is indicated by * ($P < 0.05$). Estimates are reported with (± 1 standard error).

Plant Species	**Volcanic**		**Karstic**	
	D	**U**	**D**	**U**
Alchornea latifolia	0.74 ± 0.03	0.74 ± 0.05	1.00 ± 0.00	0.74 ± 0.04*
Guarea guidonea	0.81 ± 0.02	0.92 ± 0.02*	0.95 ± 0.02	0.82 ± 0.03*
Ocotea leucoxylon	0.91 ± 0.04	0.95 ± 0.03	0	0
Syzygium jambos	0.90 ± 0.009	0.91 ± 0.01	0	0

Table 9. Average growth (increase in height in cm) of seedlings of four plant species in disturbed (D) and undisturbed (U) study sites in north-central Puerto Rico (± 1 standard deviation). Growth rates were much higher in disturbed plots than undisturbed plots in *Alchornea* and *Guarea* (*: $p<0.005$), and higher in undisturbed montane plots for the exotic species *Syzgium jambos* (**:$p < 0.005$). Sample sizes for *Ocotea* were too low for statistical significance.

Plant Species	**Volcanic**		**Karstic**	
	D	**U**	**D**	**U**
Alchornea latifolia	16.90 ± 1.50*	2.48 ± 4.18	23.59 ± 6.02*	3.82 ± 5.33
Guarea guidonea	5.45 ± 0.46*	2.59 ± 0.62	5.01 ± 0.99*	2.06 ± 0.76
Ocotealeucoxylon	11.98 ± 1.62	3.38 ± 1.94	5.40 ± 3. 89	6.30 ± 5.50
Syzygium jambos	3.76 ± 0.17	4.29 ± 1.58**	0	0

Table 10. Average growth (± 1 standard deviation) in basal diameter and height (in cm) of seedlings, and diameter at breast height (DBH in cm) and height (HT in m) of trees in disturbed (D) and undisturbed (U) study sites in north-central Puerto Rico for all species combined. * $P < 0.005$. (0) means no comparison was possible.

Location	**Saplings & Seedlings**		**Trees**	
	D	**U**	**D**	**U**
Basal Diameter	2.40 ± 0.05	2.08 ± 0.05*	0	0
Height	4.34 ± 0.47	0.20 ± 0.49*	0	0
DBH	0	0	0.44 ± 0.65	0.27 ± 0.53*
Height	0	0	1.13 ± 1.15	0.65 ± 0.85*

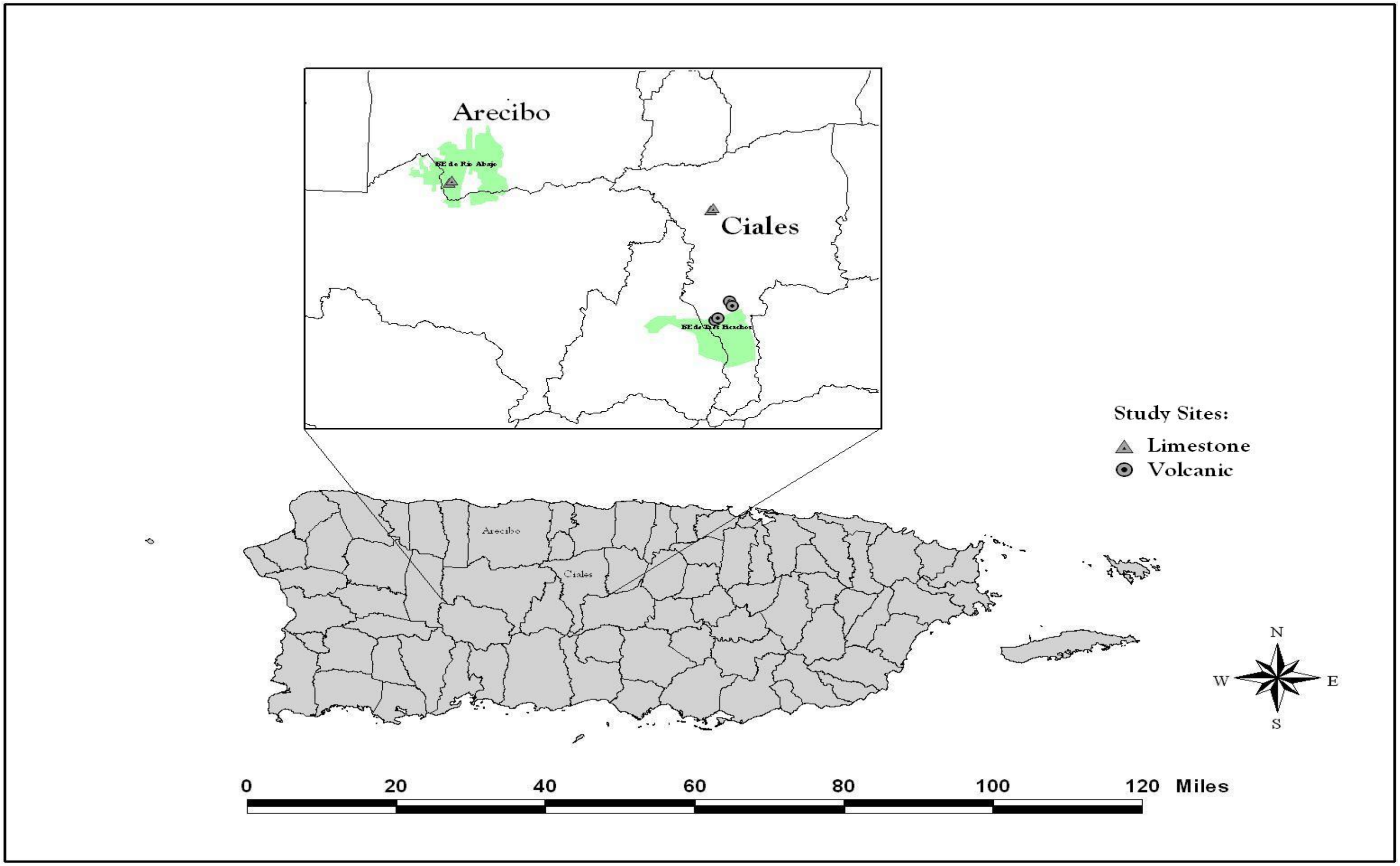

Figure 1. Location of study sites in the Volcanics and Karstic Forest of the municipalities of Ciales and Arecibo, Puerto Rico.

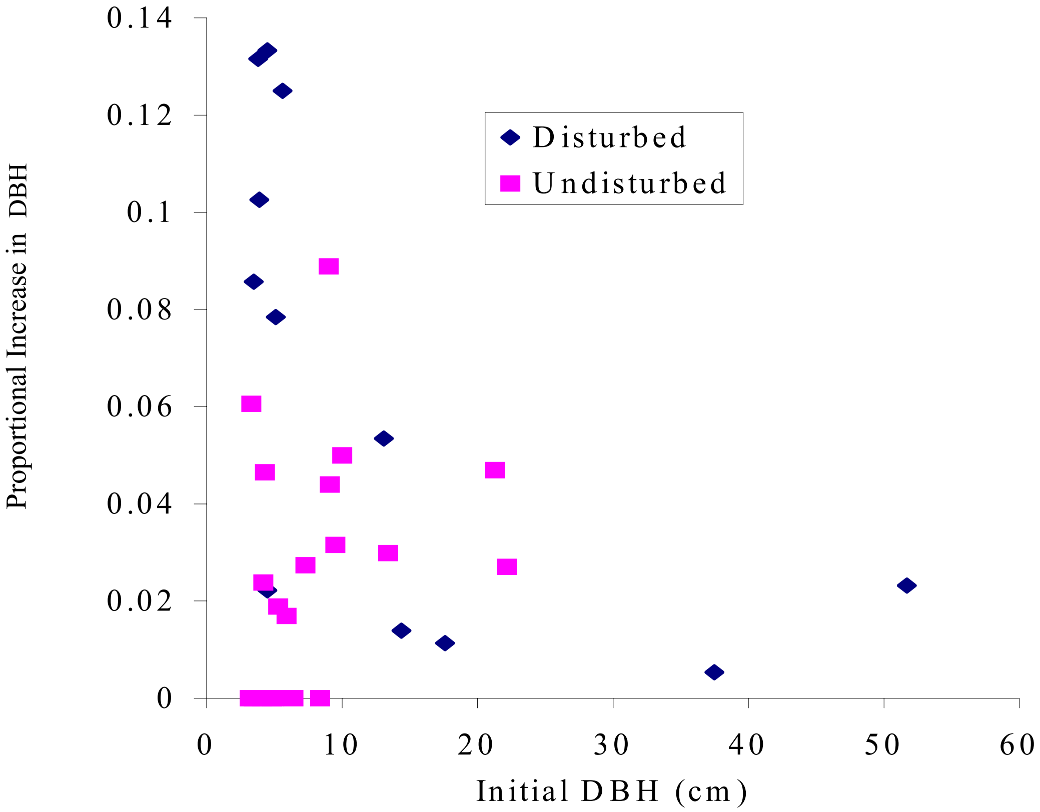

Figure 2. Growth in DBH (cm) of *Guarea guidonea* in disturbed vs. undisturbed plots.

Appendix I.

Notes on the ecology of 16 plant species used by resident birds.

The distribution of food tree species throughout the landscape can influence use patterns by avian frugivores (Carlo et al. 2003). Carlo et al. (*In press*) also showed that plant species composition and fruiting densities in abandoned coffee plantations varied between location and season, and that these differences influenced the presence/absence of avian frugivores. Studies of ecological effects of hurricanes on plant–animal interactions suggest that hurricane disturbance has a stronger impact on frugivores than insectivores (Lynch 1991, Waide 1991, Wiley and Wunderle 1993, Collazo et al. 2003). This impact has two fundamental components—immediate impact due to the hurricane, and the ensuing mortality due to loss of foraging resources (Wiley and Wunderle 1993). Collazo et al. (2003) documented that the impact of hurricane Georges on Hispaniolan Parrots (*Amazona ventralis*) released in Parque Nacional del Este was minimal (only 1 dead bird out of 25 with radio transmitters); however, mortality increased by 24% in just two months, mostly due to loss of resources.

Short-term recovery (e.g., leafing and fruiting of surviving trees), therefore, is vital for the surviving avian community. In the long-term, recruitment of food tree species and their distribution will influence the presence of and use by avian frugivores. In the aftermath of a hurricane, this process could be influenced by various factors. For example, recruitment could be facilitated by the presence of a seed bank. The creation of gaps facilitates recruitment, or replacement of plant species that were inhibited from growing by the species comprising the canopy cover prior to the disturbance. Conversely, the process could be hindered by declines in pollinators that could limit seed production, and therefore seed dispersal, of surviving trees (Pascarella 1998).

In this section, I summarize information on the distribution and recruitment ecology of sixteen plant species commonly used by avian frugivores in the north-central region of Puerto Rico. It is my hope that this summary will aid natural resource agencies in the design of habitat management plans to foster fruit resources needed by resident avian species.

Schefflera morototoni (Aubl.) Maguire, Steyerm & Frodin

Araliaceae

Schefflera morototoni is an evergreen tree of 60 feet or more in height (Little and Wadsworth 1991). *Schaefflera morototoni* is widespred in wet forest of tropical America, West Indies Cuba, Hispaniola, Puerto Rico, Virgin Islands St Thomas, St John, Tortola, Guadaloupe and Trinidad and Continental tropical America.

In Puerto Rico, *Schaefflera morototoni* grows in the subtropical wet life zone, subtropical very wet zone and subtropical pluvial zone (Ewel and Whitmore 1973), and is found scattered in forests of the lower montane moist coastal and moist limestone region of Puerto Rico (Little and Wadsworth 1991). Growth is very strong in a great variety of soils, especially that those have been abandoned after cultivation (Little and Woodbury 1976). Flowering and fruiting principally occur from October to December (Nieves 1979), although flowering can occur nearly throughout the year. Fruit development take months. In Puerto Rico, mature fruit is available in almost all year, but with a maximum production between November and June.

Schefflera morototoni exhibits behavior typical of all pioneer species, with germination and growth fast under full sun conditions and intolerance of shade conditions. This species had the maximum germination in disturbed Cialitos plot where seedlings grew in 9 quadrants. In this plot, 57 seeds germinated but only 16 seedlings survived. Germination in this site may have been facilitated by the fact that is an abandoned coffee plantation, and the trees were smaller, and of lower density, permitting sunlight to penetrate to the ground.

S. morototoni seeds have a hard seed coat, thus have the ability to remain viable in the seed bank until a canopy opening occurs, creating high light conditions favorable for seedling growth. Birds are important seed dispersers of *S. morototoni,* with around 16 species of birds in Puerto Rico commonly feeding on fruits (Ligiel in Melchior 2000). Bats are also dispersers, though less important. A study in Trinidad showed that only after the seeds have moved throughout the gizzard did the species have good germination (Liegel 2000). But when the seeds are collected and planted out of field conditions, the number of viable seeds is small and the germination is very poor (Nieves 1979).

Cordia sulcata DC.

Boraginaceae

This species, known as white manjack, is a common medium sized tree of secondary forests in the Caribbean region. White manjack seeds are dispersed by birds and bats, and commonly reach pastures and abandoned fields, as well as disturbed forest sites (Marshall 1939). This species grows in subtropical moist and subtropical wet life zone (Little and Wadsworth 1964) where the mean annual precipitation is between 1300 and 3000 mm. *Cordia sulcata* may be found growing in soils derived from limestone and various types of igneous rocks, including serpentine. The soil must be moderately well drained to well drained at both surface and subsurface layers.

Although *C. sulcata* will grow on limestone and volcanic soil, its presence (or lack thereof) in the study plots was attributable to the aspect of each site. For example, *C. sulcata* was more common in the disturbed plot of Cialitos because of its open canopy and mid-stage of succession. This study site had some remnant centennial trees, including some large adult trees of C. *sulcata* that likely produce many fruits. Once the canopy was opened by the hurricane, seeds of *Cordia* had the opportunity to grow and become established. In contrast, forests in the Tres Picachos site could be considered as being in a mature stage of succession. The closed canopy areas where the plots located had some adults trees of *C. sulcata,* but none in dominant or codominant crown positions. When *C. sulcata* is not in a dominant position and the tree is completely overtopped, individuals typically die in after a few years of suppression (Francis 2000). Germination under these conditions it practically impossible. Seedlings survive and grow in competition with brush and weeds of similar height but do not survive below a closed forest canopy (Marrero 1949, Francis 1993).

Clusia rosea Jacq.

Clusiaceae

Clusia rosea is a medium size tree commonly known as cupey. The distribution of cupey includes the Florida keys, Andros Island, Caicos in the Bahamas, the Greater Antilles, Virgins Islands, and St. Martin in the Lesser Antilles. This species can grow in different types of soils and pH's. Soil texture varies from sands to clays. *C. rosea* is more common in shallow, rocky soils in moist areas (Francis 2000). The species can be resistant to mild salt spray (Little and Wadsworth 1964), but grows most readily on the midslopes of moist limestone hills.

The only seedling found in this study was in the undisturbed Rio Abajo plot. Interestingly, there were no adult trees in the vicinity of this plot. It is possible, therefore, that the seed was dispersed by birds (Carlo et al. 2003). As cupey seedlings are moderately tolerant to shade, seedlings and saplings can survive for many years in the understory of moist secondary forest. Cupey can become established on at least three types of substrate: in soil on the forest floor, as an epiphyte in crowns of other trees, and on rocks and cliff faces. The more common means of establishment in closed forest is as an epiphyte of others trees and on rocks and cliff faces. This flexibility allows the species more avenues for recruitment than most species. Hurricanes and their slow growth rate are probably the limiting factors that prevent cupey from dominating many sites in moist forest (Francis 2000).

Andira inermis (W. Wright) DC.

Fabaceae – Papilionoideae

This species ranges widely throughout the West Indies, Greater Antilles, Lesser Antilles to Trinidad, Central America, Venezuela, Peru, Bolivia, and Brazil and has been introduced to the western part of tropical Africa. *Andira* was a component of Puerto Rico's original coastal plain and foothill forest. Today it is common in all of Puerto Rico except the upper mountains (Wadsworth 1950). Deforestation has limited mature trees to gallery forest, pastures and fencerows. In Puerto Rico, this species is adapted to a variety of sites, growing in several forest types, and is a common component of most secondary forests. *A. inermis* grows mainly in the subtropical wet and moist forests and subtropical dry forest.

Although the seedlings of *Andira inermis* are shade tolerant, they germinate better in full sunlight and grow fastest where gaps exist in the forest canopy. In germination experiments in moist limestone forest at Cambalache, saplings had grown to 1 m after 10 years (Marrero 1950). Tests in Puerto Rico showed 100 percent germination for 20 seeds sown immediately after collection (Marrero 1950). In germination experiments in wet forest in Costa Rica, sapling mortality was greater than seedling mortality (Hertwitz 1981). It was suggest that this failure of a substantial portion of the saplings to survive to maturity could be attributed to the loss of vigor and resistance associated with the attainment of reproductive maturity.

Andira was found in only two plots--undisturbed Rio Abajo and disturbed Frontón. The species is primarily bat dispersed, although it is also dispersed passively (by gravity). The disturbed Frontón site contained three adults trees, which likely were the source of seeds for the seedlings recorded in the study. The occurrence of the species in the undisturbed Rio Abajo site was likely due to bat dispersal because no matures trees were in the area.

Inga vera (Willd.)

Fabaceae – Mimosoideae

This species known locally as guaba is one of the most widely used coffee shade species in the neotropics (Little and Wadsworth 1964). The native range of guaba extends from eastern Cuba, through Jamaica, Hispaniola, and Puerto Rico (Little and Wadsworth 1964). This medium size tree is often found in wet or moist forest life zone, where annual precipitation ranges from 1000 to 4000 mm (Ewel and Whitmore 1973), but it has also been reported growing in dry areas. *Inga vera* grows in a wide range of soil types including limestone (Little and Wadsworth 1964) and at elevations of up to 1000 m above sea level.

The presence of this species in most of the study plots (e.g., abandoned coffee plantations) was due to their use for shade cover and its broad ecological tolerances. It grows very fast under full light conditions, such as those created by gaps. *Inga vera* produces vivarous seeds such that the radicule starts growing while the fruits is still on the tree and before the seed pod opens (Leon 1966). Once on the ground, the pod rots and opens, and the germination process proceeds rapidly (Francis 1994). This characteristic gives *I. vera* one advantage over the rest of the species that do not germinate until they encounter suitable conditions on the ground. Due to this *Inga vera* had particularly successful germination once a gap formed.

Inga laurina (L.) Willd.

Fabaceae– Mimosoideae

Commonly known as guama, this is a medium size tree native to the Greater Antilles and the Lesser Antilles. It is common in moist and wet forest, especially secondary forest. This tree is used as a coffee shade tree and for lumber (Francis 1994). Although *Inga laurina* is able to grow on a wide variety of soils and sites, including soils with textures from sands to clay; and can grow at different level of topography from a few meters above sea level to over 1000 m in elevation; no seedlings were recorded in any of my study plots. The seedlings are intermediate in tolerance of shade and will survive light to medium shade. *Inga laurina* produce flowers and fruits throughout the years (Little and Wadsworth 1964), and may be episodal in flowering and fruiting.

The seeds of this tree species are dispersed by bats and birds that feed on the pods (Marshall 1939). The seeds lose their viability in few weeks, and the seeds will not retain their viability if dried. In seed germination experiments, germination typically began about 5 days after sowing (Francis 1994). The growth of *Inga laurina* is fast in full sun, slower under shade. For example, in shade, the stems elongate about 6 cm before fully developing the first pairs of leaves (Francis 1994). A planting of 52 potted seedlings in a small opening in moist forest grew an average of 1m in the first 12 months and another meter in the subsequent 9 months (Francis 1994). Guama roots are endomycorrhizal, and they produce nodules, presumably associated with *Rhizobium* bacteria. One of the reasons that guama was extensively planted as coffee shade is because it fixes nitrogen through symbiotic association with *Rhizobium* bacteria in roots nodules. This advantage should help seedlings establish with high survivorship and quick growth. It seems likely that germination and light limitations, as well as dispersal limitation, may have limited germination of *Inga laurina* in the plots.

During my study, no seedlings were established in the study plots. Guama was present as a tree only in the Cialitos plots, but was not in a dominant or codominant crown position. Adult *Inga laurina* were absent from all the other plots, but mature trees were observed in Tres Picachos Plots less than 100 m away from the transect.

Casearia arborea (L.C. Rich.) Urban

Flacourtiaceae

The natural distribution of *Casearia arborea* includes Cuba, Hispaniola, Puerto Rico, Central America, and also South America (Little and Wasworth 1991). It is an evergreen tree that can grow up to 8.8 m tall. *C. arborea* is abundant and widely distributed along roadsides and in openings, thickets, and forest, in the lower mountains, moist limestone, and moist coastal regions of Puerto Rico (Little and Wadsworth 1991). However, in this study, *C. arborea* was present only in the undisturbed Cialitos plots in volcanic soils. This species is present in the karstic region of north-central Puerto Rico and has been reported as occasional to common in valley forests (Acevedo and Axelrod 1999).

Casearia guianensis (Aubl.) Urban, ***C. sylvestris*** Sw. & ***C. decandra*** Jacq.

Flacourtiaceae

These three species of the Flacourtiaceae family are very common and widely distributed in Greater Antilles and Lesser Antilles, Virgin Islands also Central and some regions of South America (Little and Wadsworth 1991). These species are shrubs or small trees of 8 to 19 m high. They are common in open areas, roadside, moist coastal, lower mountains and also in forest understory, they flowering and fruit throughout the year. (Little and Wadsworth 1991).

C. guianensis was not present in any study plot; *C. sylvestris* occurred as saplings or small trees in disturbed Rio Abajo and disturbed Frontón plots, and only one sapling of *C decandra* was recorded in undisturbed Frontón. *Casearia sylvestris*, *C. guianensis* and *C decandra* are reported by Acevedo 1999 as common in karst valley forest and hillsides.

C. guianensis, *C. sylvestris* and *C. decandra* are species that grow better in full sun light and secondary forest. The fruit production of these species is higher in forests with an open canopy or in places where the canopy is not high (personal observation).

Ocotea leucoxylon (Sw.) Lanessan

Lauraceae

Ocotea leucoxylon, or laurel geo, is one of the most common laurels in Puerto Rico. It is a small to medium sized evergreen tree that reaches a maximum height of 18 m (Little and Wadsworth 1991). *O. leucoxylon* is widely distributed in moist coast, moist limestone, and volcanic forests of the island. It is distributed throughout the Greater Antilles and the Lesser Antilles from Montserrat to Grenada, Trinidad and Tobago, and also in St. Thomas and Tortola.

Laurel geo flowers and fruits irregularly through the year (Little and Wadsworth 1991). Its seeds are dispersed by birds, and commonly reach pastures, abandoned fields, as well disturbed forest (Little and Wadsworth 1991).

In my study, growth in shade was very slow in contrast to that in gaps or forest edges (personal observation). Seedlings and saplings survived in all of the undisturbed plots, but growth of the seedlings in full shade was very slow. This species was recorded in all plots, but was more abundant in volcanic soil plots, where the species was found in humid, deep soils.

Ocotea floribunda (Sw.) Mez

Lauraceae

Ocotea floribunda is a small to medium sized evergreen tree that can grow up to 60 feet tall. It is found throughout the Greater Antilles, including St. John, Tortola, and

Lesser Antlilles from Guadalupe to Grenada, and Trinidad. Flowering and fruiting occurs from October to July (Little and Wadsworth 1991)

This species was present in 5 of 8 plots and was more common in the undisturbed Rio Abajo site, where it grew in 8 of 10 quadrants. *Ocotea floribunda* is a species that tolerates shade extremely well, as do others members of the family. In the understory, *O floribunda* and *Ocotea leucoxylon* were the most common species of Lauraceae. Trees up to 13 m were observed close to the Rio Abajo plot, where the species is reported as occasional (Acevedo 1999). This species is restricted to the moist valley forest in the limestone by the deep soils and the presence in the hills is very rare (personal observation).

Miconia prasina (Sw.) DC. and ***Miconia serrulata*** (DC.) Naudin

Melastomataceae

In Puerto Rico, most of the Melastomataceae are woody shrubs, although there are also several primary forest trees and a few herbs (Little and Wadsworth 1964). The majority of the Melastomataceae in the island occur in disturbed areas in the mesic to wet montane forest zone at middle to higher elevations (Little and Wadsworth 1964, Little, et al., 1974; Liogier and Martorell 1982)

Miconia prasina is a small tree that grows up to 8 m tall. It is very common throughout the Greater Antilles, Lesser Antilles and Tropical America. In Puerto Rico, it is common in moist coastal, moist limestone, and lower montane forests (Little and Wadsworth 1991).

Miconia prasina is common in the open valleys in Rio Abajo Forest. Acevedo (1999) described the species as occasional to locally common in disturbed areas and fields. In the Rio Abajo sites, the species was common in open, or in disturbed areas. It is one of the most common species in the transitions areas between the teca and mahoes plantations, disturbed areas that were affected strongly by hurricane Georges (personal observation).

Miconia serrulata is an evergreen shrub/small tree that can grow up to 8-12 m. It is common throughout of the Greater Antilles, Santa Cruz, Mexico to Panama and South America from Colombia to Brasil, Bolivia and Peru. It flowers and fruits in the spring or irregularly throughout the year. The species is uncommon throughout Puerto Rico (Little et al. 1974). In the Rio Abajo Forest, Acevedo (1999) reports it as present, but not common. *M. serrulata* is restricted to humid soils between limestone and ravines (personal observation) and is not part of the indigenous flora of the limestone hill or mogotes.

Guarea guidonea (L.) Sleumer

Meliaceae

Guarea guidonea is an evergreen tree with a spreading crown and dense foliage. It is reported as native in Cuba, Hispaniola, and Puerto Rico (Little and Wadsworth 1991), St Croix and Trinidad (Marshal 1939), in the Caribbean and Nicaragua (Taylor 1963), Costa Rica (Weaver 2000), and South America (Weaver 1986). It grows in humid to wet subtropical and tropical regions. Known as guaraguao in Puerto Rico, today it is found throughout the lower montane, moist limestone, and moist coastal regions of the Islands. *Guarea* is one of the most common trees in Puerto Rican coffee plantations in humid and wet secondary forest of the central mountains (Birdsey and Weaver 1982). *G. guidonea* reaches the upper canopy on favorable sites, but is not a dominant tree in the forests of

Puerto Rico (Marrero 1948). Seedlings and saplings of this tree species were present in all plots in this study. It was recorded in 67 of 80 quadrants sampled within plots.

Guarea guidonea is a species principally adapted to withstand shade as a seedling and understory tree. Yet, its regeneration in the closed canopy of the subtropical wet forest of Luquillo Mountains is rare (Weaver 1990); however, suggesting that small gaps in the canopy, possibly caused by hurricanes, may facilitate its growth. In a study of regeneration and understory survival of 29 species that reach canopy size in the subtropical wet forest of the Luquillo Mountains, understory trees of *Guarea* were relative common whereas seedlings were relative scarse (Smith 1970). This suggests that *Guarea* regeneration might be related to a past disturbance of the forest.

Cecropia schreberiana Miq.

Moraceae

Cecropia schreberiana is one of the most abundant trees in Puerto Rico. It is a dioecious, medium size evergreen tree that reaches a height of 21 m and 6 dm in diameter. The species is deciduous in areas with a pronounced dry season (Little and Wadsworth 1991). It has a wide range throughout West Indies from Cuba and Jamaica to Trinidad and Tobago. A pioneer species, it is found abundantly in open areas and in both primary and secondary forest. The species is found throughout Puerto Rico and the Virgin Islands, with the exception of dry coastal and dry limestone regions.

I found *Cecropia* seedlings in 6 of the 8 study plots. They were more common in undisturbed Fronton plot where yagrumo is more abundant and the canopy was open over a significant area. *C. schreberiana* is a pioneer tree species that requires nearly full sunlight to germinate and grow. The species commonly covers openings quickly resulting from selective harvest of trees in the forest. Little and Wadsworth (1991) observed growth rates of 1.8 m in 7 months and 2.1 m in one year. Its open canopy provides a good environment for the development of a new forest, where sun intolerant species can flourish, and grow relatively rapidly in the sunlight filtered through its canopy.

Cecropia flowers throughout the year, with a maximum production of fruits in the dry season. Reproductive maturity occurs between 3 and 5 years, depending on whether the tree has pistillate or staminate flowers and the proximity of surrounding vegetation (Silander 1979). The species produces prodigious quantities of seed: approximately 5,000,000 seeds per kilogram of wet fruit mass, seeds germinate at a rate of 80% in humid, lighly shade conditions (Silander 1979), although exact seed production depends on a variety of factors including height and age of the tree. In Puerto Rico, the mature fruits of the *Cecropia schreberiana* are dispersed by 15 species of bird and bats (Leck 1972, Silander 1979). The seeds once in the ground show low viability due to embryo damage by fungus and insects, and are typically viable only 2 to 3 months (Silander 1979).

Appendix II. List of Species identified in the study sites

Woody and non woody species identified during one year period at eight transects. Transects: Dist. Cia. = Disturbed Cialitos, Und. Cia. = Undisturbed Cialitos, Dist. T. Pi. = Disturbed Tres Picachos, Und.T. Pi. = Undisturbed Tres Picachos, Dist. R. En. = Disturbed Rio Encantado, Und. R. En. = Undisturbed Rio Encantado, Dist. R. Ab. = Disturbed Rio Abajo, Und. R. Ab. = Undisturbed Rio Abajo

Taxonomy	**Growth Habit**	**Dist. Cia.**	**Und. Cia.**	**Dist. T. Pi.**	**Und. T. Pi.**	**Dis. R. En.**	**Und. R. En.**	**Dis. R. Ab.**	**Und. R. Ab.**
Acanthaceae									
Ruellia Coccinea (L.) Vahl.	Herb	0	0	1	0	1	1	0	0
Amaranthaceae									
Iresine angustifolia H. & B. ex. Willd.	Herb	0	0	1	0	1	0	0	0
Anacardiaceae									
Comocladia glabra (Schultes) Spreng.	Tree	0	0	0	0	0	0	1	0
Spondias mombin L.	Tree	0	0	0	0	16	0	0	0
Apocynaceae									
Forsteronia portoricensis Woodson	Vine	0	1	0	0	0	0	1	0
Araceae									
Anthurium dominicense Schott	Herb	0	0	0	0	1	0	0	0
Anthurium scandens (Aubl.) Engl.	Herb	1	0	0	1	0	0	0	0
Dieffenbachia seguine (Jacq.) Schott	Herb	1	0	1	1	0	0	0	0
Phylodendron angustatum Schott	Vine	0	0	0	0	1	0	0	0
Xanthosoma undipes (C. Koch) C. Koch	Herb	0	0	0	1	0	0	0	0
Araliaceae									
Dendropanax arboreus (L.) Dec. & Plan.	Tree	0	1	0	1	1	1	1	0
Schefflera morototoni (Aubl.) Mag. et al.	Tree	55	0	0	0	0	0	4	0

Continued

Taxonomy	Growth Habit	Dist. Cia.	Und. Cia.	Dist. T. Pi.	Und. T. Pi.	Dis. R. En.	Und. R. En.	Dis. R. Ab.	Und. R. Ab.
Asclepiadaceae									
Gonobolus stephanotrichus Grisebach	Vine	0	0	0	0	1	0	0	0
Asteraceae									
Mikania cordifolia (L.F.) Willd.	Vine	0	0	0	0	P	0	0	0
Mikania sp. # 1	Vine	P	P	P	0	0	0	0	0
Mikania sp. # 2	Vine	0	0	0	0	P	P	0	0
Pluchea carolinensis (Jacq.) G. Don	Shrub	0	0	0	0	1	0	0	0
Elephanthopus mollis Kunth. in HBK.	Herb	1	1	0	0	0	0	0	1
Erechtites hieracifolia (L.) Raf. Ex. DC.	Herb	1	0	1	0	0	0	0	0
Eupatorium odoratum L.	Shrub	1	0	0	0	0	0	0	0
Vernonia sp.	Herb	1	0	0	0	0	0	0	0
Bignoniaceae									
Macfadyena unguis-cati (L.) A. Gentry	Vine	1	1	1	0	1	1	0	0
Menispermaceae									
Cissampelos pareira L.	Vine	0	0	1	1	0	0	1	0
Boraginaceae									
Cordia sulcata DC.	Tree	16	7	0	0	1	0	1	0
Tournefortia hirsutissima	Vine	0	0	1	0	0	0	0	0
Bromeliaceae									
Guzmania sp.	Herb	0	1	0	0	0	0	0	0
Pitcairnia angustifolia O.F. Cook	Herb	0	0	0	0	0	P	0	0
Tillandsia fasciculata Sw.	Herb	1	1	0	1	0	0	0	0

Continued

Taxonomy	**Growth Habit**	**Dist. Cia.**	**Und. Cia.**	**Dist. T. Pi.**	**Und. T. Pi.**	**Dist. R. En.**	**Und. R. En.**	**Dist. R. Ab.**	**Und. R. Ab.**
Combretaceae									
Buchenavia tetraphylla (Aublet) Howard	Tree	12	0	0	1	0	0	0	0
Commelinaceae									
Commelinopsis glabrata R. D. Hunt	Herb	P	P	P	P	0	0	0	0
Convolvulaceae									
Ipomoea tiliacea (Wild.) Choisy	Vine	P	0	P	0	0	0	0	0
Cucurbitaceae									
Melothria pendula L.	Vine	P	0	0	0	0	0	0	0
Momordica charantia L.	Vine	0	0	0	0	P	0	0	0
Cyatheaceae									
Cyathea arborea L.	Tree	0	0	1	0	0	0	0	0
Cyathea horrida (L.) Presl	Tree	1	0	0	0	0	0	0	1
Cyathea portoricensis Spreng. ex Kuhn	Tree	1	0	0	1	0	0	0	0
Cyathea tenera (J. Smith ex Hook) Moore	Tree	0	0	0	1	0	0	0	0
Cyperaceae									
Cyperus odoratus L.	Herb	0	1	0	0	0	0	0	0
Scleria sp.	Herb	0	1	0	0	0	0	0	0
Dioscoreaceae									
Dioscorea alata L.	Vine	0	0	0	1	0	0	0	0
Dioscorea pilosiuscula Bert. ex Spreng.	Vine	0	0	0	0	1	0	0	0
Rajania cordata L.	Vine	1	1	0	0	0	0	0	0

Continued

Taxonomy	**Growth Habit**	**Dist. Cia.**	**Und. Cia.**	**Dist. T. Pi.**	**Und. T. Pi.**	**Dist. R. En.**	**Und. R. En.**	**Dist. R. Ab.**	**Und. R. Ab.**
Alchorneopsis floribunda (Benth.) Muell. Arg.	Tree	1	1	0	0	0	0	0	0
Drypetes laterifolia (Sw.) Krug & Urban	Tree	0	0	0	0	1	0	0	0
Bignoniaceae									
Tabebuia heterophylla (DC.) Britt	Tree	0	0	0	0	0	0	0	1
Bombacaceae									
Quararibea turbinata (Sw.) Poir	Tree	0	0	0	0	0	1	0	0
Boraginaceae									
Cordia alliodora (R. & P.) Oken	Tree	1	0	0	0	0	0	0	0
Cordia polycephala (Lam.) I. M. Johnst.	Shrub	1	0	1	1	0	0	0	0
Musaseae									
Musa sapientum L.	Herb	0	0	1	0	0	0	0	0
Flacourtiaceae									
Casearia arborea (L. C. Rich.) Urban	Tree	1	7	0	0	0	0	0	0
Casearia decandra Jacq.	Tree	0	0	0	0	0	0	0	1
Casearia sylvestris Swartz	Tree	1	1	0	0	1	0	1	1
Homalium racemosum Jacq.	Tree	0	0	0	0	0	1	0	0
Gesneriaceae									
Gesneria cuneifolia (A. P. DC.) Fritsch	Herb	0	0	0	0	0	P	0	0
Guttiferae									
Calophyllum antillanum Britton	Tree	0	0	0	0	74	2	15	10
Clusia rosea Jacq.	Tree	0	1	0	0	0	0	0	0

Continued

Taxonomy	**Growth Habit**	**Dist. Cia.**	**Und. Cia.**	**Dist. T. Pi.**	**Und. T. Pi.**	**Dist. R. En.**	**Und. R. En.**	**Dist. R. Ab.**	**Und. R. Ab.**
Lauraceae									
Cinnamomun elongatun (Nees) Kost.	Tree	5	0	5	2	0	0	0	0
Ocotea floribunda (Sw.) Mez	Tree	0	0	2	0	2	2	3	13
Ocotea leucoxylon (Sw.) Lanessan	Tree	17	20	14	7	0	0	5	1
Malpighiaceae									
Malpighia coccigera L.	Shrub	0	0	0	0	0	1	0	0
Byrsonima spicata (Cav.) HBK.	Tree	6	2	0	0	0	0	0	0
Malvaceae									
Hibiscus elatus Sw.	Tree	0	0	0	0	0	0	0	62
Pavonia spinifex (L.) Cav.	Shrub	0	0	0	0	0	1	0	0
Thespesia grandiflora DC.	Tree	0	0	0	0	0	0	0	1
Marattiaceae									
Danaea elliptica J.E. Smith	Herb	P	P	0	0	0	0	0	0
Marcgraviacea									
Marcgravia brittoniana Alain	Herb	0	0	0	0	P	0	0	0
Melastomataceae									
Henriettea sp.	Tree	0	1	0	0	0	0	0	0
Miconia laevigata (L.) DC.	Tree	0	0	0	0	1	1	1	1
Miconia prasina (Swartz)DC.	Tree	0	8	0	0	0	0	5	0
Miconia racemosa (Aublet) DC.	Shrub	0	0	0	1	0	0	0	1
Miconia serrulata (DC.) Naudin	Tree	1	2	1	1	0	0	0	0
Miconia sp.	Tree	0	0	1	1	0	0	0	0

Continued

Taxonomy	**Growth Habit**	**Dist. Cia.**	**Und. Cia.**	**Dist. T. Pi.**	**Und. T. Pi.**	**Dist. R. En.**	**Und. R. En.**	**Dist. R. Ab.**	**Und. R. Ab.**
Moraceae									
Cecropia schreberiana Miq.	Tree	0	0	3	0	25	6	9	1
Myrsinaceae									
Myrcine coriacea (Sw) R. Br.	Tree	0	7	0	2	0	0	0	0
Ardisia obovata Desv. ex Hamilton	Tree	0	0	0	0	1	0	0	
Myrtaceae									
Eugenia confusa DC.	Tree	0	0	0	0	5	1	0	0
Eugenia monticola (Sw.) DC.	Tree	0	0	0	0	148	12	0	0
Myrcia splendens (Swartz) DC.	Tree	3	7	0	3	0	0	0	0
Syzygium jambos (L.) Alst.	Tree	460	215	1	15	0	0	0	0
Nyctaginaceae									
Pisonia aculeata L.	Shrub	0	0	0	0	0	0	0	1
Orquidaceae									
Oecoeoclades maculata (Lindley) Lind.	Herb	0	P	0	P	P	P	0	P
Polystachya foliosa (Hook) Reich. F.	Herb	0	0	0	0	0	0	0	P
Arecaceae									
Prestoea montana (Graham) Nichols	Tree	1	1	1	1	0	0	0	0
Passifloraceae									
Passiflora edulis Sims	Vine	P	0	0	0	0	0	0	0
Passiflora rubra L.	Vine	0	0	0	0	0	0	P	0
Passiflora sp.	Vine	1	0	0	0	0	0	0	0

Continued

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Piperaceae									
Piper amalago L.	Tree	0	0	0	0	0	8	1	0
Piper hispidium Sw.	Shrub	1	0	0	0	0	0	1	0
Piper jacquemontianum Kunth	Shrub	0	1	0	0	0	0	1	0
Piper marginatum Jacq.	Shrub	0	4	0	0	0	0	0	0
Piper swartzianum (Miq.) C.DC.	Shrub	0	0	0	5	0	0	0	0
Poaceae									
Ichnanthus pallens (Sw.) Munro	Herb	P	P	P	P	P	P	0	P
Lasiasis divaricata (L.) Hitchc.	Herb	P	0	0	0	P	0	0	P
Unknown # 1	Herb	0	0	P	0	0	0	0	0
Unknown # 2	Herb	0	0	P	0	0	0	0	0
Unknown # 3	Herb	0	0	P	0	0	0	0	0
Unknown # 4	Herb	0	P	0	0	0	0	0	0
Unknown # 5	Herb	0	0	0	P	0	0	0	0
Polygalaceae									
Securidaca virgata Sw.	Vine	P	P	0	P	P	P	P	P
Moraceae									
Ficus stahlii Warb. in Urb.	Tree	0	0	0	0	8	0	0	0
Polygonaceae									
Coccoloba costata Wr. ex Sauv.	Tree	0	0	0	0	1	0	0	0
Polypodiaceae									
Adiantum pyramidale (L.) Willd. in L.	Herb	P	P	0	P	0	P	0	P
Adiantum tenerum Sw.	Herb	0	0	0	0	P	P	0	0
Arachnoides chaerophylloides (Poir.) Proc.	Herb	0	0	0	0	0	0	0	0

Continued

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Asplenium trichomanes-dentatum L.	Herb	0	0	0	0	0	P	0	0
Asplenium abscisum Willd. in L.	Herb	0	0	0	0	0	P	0	0
Asplenium cristatum Lam.	Herb	0	0	0	0	P	P	0	0
Blechnum occidentale L.	Herb	P	P	P	P	0	0	0	P
Ctenitis hirta (Sw.) Ching	Herb	0	0	0	0	0	P	0	0
Ctenitis nemorosa (Willd.) Copel	Herb	0	0	0	0	0	P	P	0
Ctenitis subincisa (Willd.) Ching	Herb	0	0	0	P	0	0	0	0
Denstaedtia bipinata (Cav.) Maxon	Herb	0	0	0	P	0	0	0	0
Nephrolepis exaltata (L.) Schott	Herb	0	P	0	0	P	0	0	P
Pitirograma calomelanos (L.) Link	Herb	0	0	0	0	P	0	0	0
Polypodium astrolepis Liemb.	Herb	P	0	0	0	0	0	0	0
Polypodium lycopodioides J.S. Smith	Herb	0	P	P	0	0	0	0	0
Pteris tripartita Sw.	Herb	0	0	0	0	P	0	0	0
Pteris vitata L.	Herb	0	0	0	0	P	0	0	0
Tectaria heracleifolia (Willd.) Under.	Herb	0	0	0	0	P	P	0	0
Tectaria incisa Cav.	Herb	0	0	0	P	0	0	P	0
Thelypteris balbisii (Spreng.) Ching	Herb	0	0	0	0	P	0	P	0
Thelypteris poiteana (Boris) Proctor	Herb	0	0	0	0	P	0	0	0
Rhamnaceae									
Colubrina arborescens (Miller) Sarg.	Tree	0	0	0	0	0	1	0	0
Gouania lupuloides (L.) Urban	Vine	0	0	0	0	P	0	0	0
Rosaseae									
Prunus myrtifolia (L.) Urban	Tree	0	0	1	0	0	0	0	1
Rubiaceae									
Chioccoca alba (L.) Hitchc.	Vine	0	0	0	0	1	1	0	1
Coccopsypselum herbaceum P. Browne	Herb	P	P	0	0	0	0	0	0

Continued

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Coffea arabica L.	Tree	49	1	62	58	9	1	0	0
Psychotria berteroana DC.	Shrub	58	28	0	1	0	0	0	0
Psychotria brachiata Sw.	Shrub	1	1	0	1	0	0	0	1
Psychotria deflexa DC.	Shrub	0	1	0	0	0	0	0	0
Rutaceae									
Citrus aurantium L.	Tree	0	0	0	1	0	0	0	0
Zanthoxylum martinicense (Lam.) P. Wil.	Tree	2	0	0	0	8	3	1	3
Sabiaceae									
Meliosma herbertii Rolfe	Tree	1	0	1	0	0	0	0	0
Sapindaceae									
Paullinia pinnata L.	Vine	0	0	0	P	0	0	0	0
Serjania polyphylla (L.) Radlk.	Vine	0	0	0	0	P	P	0	P
Simarubaceae									
Picramnia pentandra Sw.	Tree	0	0	0	0	0	0	4	0
Smilacaceae									
Smilax dominguensis Willd.	Vine	0	0	0	0	P	P	0	P
Solanaceae									
Capsicum frutescens L.	Shrub	0	0	0	0	1	0	0	0
Cestrum macrophyllum Vent.	Shrub	0	1	1	0	0	0	0	0
Solanum rugosum Dunal in DC.	Shrub	23	1	1	0	0	0	0	0
Staphyleaceae									
Turpinia occidentalis (Sw.) G. Don.	Tree	0	28	0	0	0	0	0	0

Continued

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Ulmaceae									
Trema micrantha (L.) Blume	Tree	0	0	0	0	1	0	0	0
Urticaceae									
Pilea obtusata Liem.	Herb	0	0	P	0	0	P	0	0
Urera baccifera (L.) Wedd.	Shrub	0	0	6	0	1	0	0	0
Vitaceae									
Cissus verticillata (Aublet) Howard	Vine	0	0	0	P	P	0	P	0
Rubiaceae									
Gonzalagunia hirzuta (Jacq.) K. Schum.	Shrub	0	0	0	0	0	1	0	0
Palicourea crocea (Sw.) Roem. & Schul.	Shrub	1	0	0	0	0	0	0	0
Fabaceae									
Andira inermis (W. Wr.)	Tree	1	0	0	0	2	0	5	0
Desmodium axillare (Sw.) DC.	Herb	0	P	P	P	0	0	P	P
Erytrina poeppigiana (Walp.) O.F. Cook	Tree	0	0	0	1	0	0	1	0
Inga vera Willd.	Tree	0	0	169	1	1	0	64	0
Teramnus uncinatus (L.) Sw.	Vine	0	0	0	0	0	0	0	P
Arecaceae									
Coccothrinax alta (O.F. Cook) Becc	Tree	0	0	0	0	0	1	0	0
Roystonea borinquena F. Cook	Tree	0	0	0	0	1	1	0	1
Hippocrateaceae									
Hippocratea volubilis (L.)	Tree	0	0	0	0	P	P	0	0
Meliaceae									
Guarea guidonea (L.) Sleumer	Tree	28	18	204	126	22	70	21	19

Continued

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Trichillia pallida Sw.	Tree	0	0	0	0	21	2	0	0
Phytolacaceae									
Phytolacca rivinoides Kunth & Bouche	Herb	1	0	0	0	0	0	0	0
Trichostigma octandrum (L.) H. Walt.	Vine	0	0	0	0	P	P	P	0
Burseraceae									
Tetragastris balsamifera (Sw.) Kuntze	Tree	1	4	0	0	0	0	0	0
Euphorbiaceae									
Acalypha bisetosa Bert.	Shrub	0	0	0	0	1	2	0	0
Alchornea latifolia Sw.	Tree	143	24	36	22	5	16	1	0

P= Present in transects but not were counts during the study.