POST-FIRE REGENERATION IN SUBTROPICAL DRY FOREST OF PUERTO RICO

By

Brett Wolfe

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Approved by:

Jesús Danilo Chinea, Ph.D. Member, Graduate Committee	Date
Raúl Macchiavelli, Ph.D. Member, Graduate Committee	Date
Jarrod Thaxton, Ph.D. Member, Graduate Committee	Date
Skip J. Van Bloem, Ph.D. President, Graduate Committee	Date
José L. Perdomo, Ph.D. Representative of Graduate Studies	Date
Miguel Muñoz, Ph.D. Chairperson of the Department	Date

Abstract

Dry forests were widespread in the tropics before being cleared for agricultural and urban use, but they are now considered to be one of the most endangered ecosystem types. Cleared and degraded tropical dry forests commonly form exotic-grassland communities that are maintained by periodic fires and are difficult to reforest. In the dry zone of southwest Puerto Rico, exotic grasses invade disturbed areas and expand into intact forest through successive burning. When fire is prevented in such areas they are colonized by the exotic legume tree *Leucaena leucocephala,* which dominates the canopy for >80 yr. A better understanding of the factors that drive these vegetative patterns is needed to improve management aimed at forest restoration and protection. This project assessed the fire resistance of common tree species, the seed rain in degraded forest areas, and the performance of saplings in repeatedly burned areas of Guánica Forest. Bark thickness was measured on 474 trees of 26 species and related to stem size. Most species obtained putative fire-resistant bark thickness only in the largest trees or not at all, while two species, *Bursera simaruba* and *Bucida buceras* obtained it in relatively small stems. Seed rain was collected with 100 traps of 0.25-m² for one year (beginning July 2007) at four sites that had five focal vegetation types along a gradient of degradation. The seed count totaled 35,610 non-graminoid seeds. Seed rain of native trees and *L. leucocephala* were similarly low in open grass areas. Exotic-forest areas, dominated by *L. leucocephala,* had an increased density of animal-dispersed tree seeds compared to open grass areas. Planted saplings were used to compare growth and survival in the forest understory to grass-dominated areas with and without protection from fires. In November 2007, 455 saplings of 13 native tree species and *L. leucocephala* were planted in three areas dominated exotic grasses and in nearby forest. Survival of the burned saplings was initially high (36.4%), but eight months later few survived. The majority died during a seasonal drought in June - July 2008. In the same period sapling survival in the unburned grasslands was reduced compared to forests. Growth during the first year was minimal and dieback was common on shoots of surviving saplings. An exception was *L. leucocephala* in the unburned grasslands, which on average grew 11.7 mm in diameter and 30.0 cm height. These results suggest that native trees are not resistant to fire at sapling or adult sizes, and they are ineffective for reforestation of burned sites in Guánica Forest. The use of *L. leucocephala* as an intermediary between exotic grassland and native forest is suggested.

Resumen

Los bosques secos eran abundantes en los trópicos antes de la intervención del ser humano; no obstante actualmente son uno de los ecosistemas en mayor peligro. Cuando los bosques secos son cortados o degradados entonces forman pastizales exóticos, mantenidos por fuegos periódicos y difíciles de reforestar. En la zona seca del suroeste de Puerto Rico, las gramas exóticas invaden áreas perturbadas y se extienden adentro de bosques intactos mediante fuegos sucesivos. En las áreas de pastizal donde se previenen los fuegos, el árbol leguminoso exótico *Leucaena leucocephala,* coloniza y domina la copa durante >80 años. Es necesario un mejor conocimiento de los factores que determinan estos patrones vegetativos para mejorar el manejo dirigido a la protección y restauración del bosque. Este proyecto evaluó la resistencia al fuego de especies de árboles comunes, la lluvia de semillas en las áreas degradadas del bosque, y el rendimiento de las plántulas en áreas donde hubo fuegos repetidos en el bosque seco de Guánica. El grosor de la corteza se midió en 474 árboles de 26 especies y se relacionó con el tamaño del tallo. La mayoría de las especies solo obtuvieron la corteza con el grosor resistente a fuego cuando los tallos eran grandes mientras otros nunca la presentaron. Dos especies, *Bursera simaruba* y *Bucida buceras,* la obtuvieron en tallos relativamente pequeños. La lluvia de semillas se colectó con 100 trampas de 0.25 m² durante un año (julio 2007 – junio 2008) en cuatro sitios que tenían cinco tipos de vegetación a lo largo un gradiente de degradación. Se contaron 35,610 semillas no-graminoides. La lluvia de semillas de árboles nativos y *L. leucocephala* fueron similares y bajas en las pastizales. En boques dominados por *L. leucocephala* la lluvia de semillas dispersadas por animales aumentó comparado con pastizales. En noviembre 2007, 455 plántulas de 13 especies de árboles nativos y *L. leucocephala* se sembraron para comparar su rendimiento en el sotobosque y pastizales sin y con protección contra fuegos. La sobrevivencia de las plántulas quemadas fue inicialmente alta (36.4%), pero ocho meses más tarde pocas quedaron vivas. La mayoría murieron durante una sequía temporal en junio – julio 2008 que también bajó la sobrevivencia en las pastizales no quemados comparado con bosques. El crecimiento durante el primer año fue mínimo o negativo, excepto *L. leucocephala* en pastizales no quemados, que creció en promedio 11.7 mm en diámetro y 30.0 cm en altura. Estos resultados sugieren que los árboles nativos no son resistentes a fuegos como plántulas o adultos y que no son efectivas para reforestaciones en Guánica. Se recomienda el uso de *L. leucocephala* como un intermediario entre pastizales exóticos y bosques nativos.

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Chapter 1
Introduction to Thesis

Fire is incredibly influential in structuring ecosystems. Requiring only three ingredients – fuel, oxygen, and ignition – it is able to maintain unique assemblages of plants on scales of square meters to entire continents (Bond et al. 2004). A fire's effect on an ecosystem depends on a variety of factors – intensity, duration, frequency, seasonality, and size of the fire – termed the fire regime (Whelan 1995). Fire regimes are in turn dependent on the climatic, geologic, and topographic features of the area. Patterns of temperature and rainfall, along with edaphic features, determine plant productivity, desiccation, decomposition, and ultimately fuel loads. Natural sources of ignition – lightning, rock falls, and volcanic eruptions – also vary geographically. Humans have shaped fire regimes for millions of years by igniting fires to aid in hunting and food production (Bond and van Wilgen 1996). Increased fire frequencies have followed human expansion on continents and islands from prehistoric to modern times. Consequently, conserving biodiversity and ecosystem function often depends on managing fire regimes.

Some highly diverse and productive plant communities depend on fire regimes that include frequent, low-intensity fires (e.g., grasslands, savannas, temperate forests). But when such fire regimes are applied to lowland tropical forests, plant communities commonly collapse and become dominated by a few plant species, often exotic (i.e., introduced to the region by humans) grasses (D'Antonio and Vitousek 1992). Although fires were long used in tropical forests as a component of swidden agriculture, their extensive use in modern times has been a major factor in the conversion of vast amounts of tropical forest to exotic grassland (Cochrane 2003). For example, the front of deforestation in the Amazon is often preceded for many miles by fires that escape into forests from slash-and-burn clearing (Cochrane 2003). This process is a major setback to efforts aimed at protecting intact forests and restoring degraded areas throughout the tropics (Janzen 1988, Elliott et al. 2003).

In the dry forest zones of Puerto Rico and the Virgin Islands, Ewel and Whitmore (1973) described fire as "common on the better soils, where successional vegetation includes many grasses, and large amounts of organic debris accumulate on the soil surface during the dry season." However, the extent to which these fires were natural or anthropogenic remains unclear.

Most of the dry forest zone in this region has been converted to other uses such as agriculture and urbanization. When degraded areas are abandoned or left unmaintained they tend to form stable grassland-savanna communities that are maintained by periodic fires and are difficult to reforest (Francis and Parrotta 2006). When fire is prevented in such areas, they become colonized by the exotic legume tree *Leucaena leucocephala,* which dominates the canopy for >80 yr (Weaver and Chinea 2003, Francis and Parrotta 2006, Molina Colón and Lugo 2006, Pérez Martínez 2007, Weaver and Schwagerl 2008). About 4% of the zone remains forested, of which 80% is protected within the Guánica State Forest and Biosphere Reserve (Guánica Forest) (Murphy et al. 1995). Natural fires have not been recorded in Guánica Forest, although human-caused fires are common around the periphery and along roadside areas within the forest (Murphy et al. 1995; M. Canals, personal communication).

Managers have taken measures to prevent and contain wildfires in Guánica Forest. Since 1986, prescribed fires have been used to prevent uncontrolled fires from entering intact forest areas along the coastal road Rt. 333. These activities have been coordinated with local and regional forest fire fighters since 2003. The efforts have had success in limiting the extent of uncontrolled burning, yet wildfires continue to burn and extend into intact forest (Canals 2007). Little information is available on how these fires are impacting vegetation. Although successional patterns have been well described in the local secondary forests, the ecological factors that drive these patterns are not well understood (Weaver and Chinea 2003, Francis and Parrotta 2006, Molina Colón and Lugo 2006, Pérez Martínez 2007, Weaver and Schwagerl 2008). This thesis was designed to address this shortage, to provide a basis for predicting future plant communities in burned areas, and to develop techniques for managing them. Specifically, my thesis assesses 1.) fire resistance of native trees using bark characteristics, 2.) seed rain in degraded areas, and 3.) sapling performance in repeatedly-burned areas.

Thesis layout

This thesis is divided into three main chapters. Each describes a project with separate datasets and hypotheses that is intended to be submitted for publication in a peer-reviewed journal. A concluding chapter synthesizes the major findings of the entire research and provides overall management considerations. Below is a general description of the study site. It is

provided here to prevent repetition in the data chapters. The methods section of each chapter elaborates upon the site description as needed to detail the specifics of each project.

Study Site

Guánica Forest (17˚58'N, 66˚55'W) is located in the subtropical dry forest zone of southwest Puerto Rico that is formed by the rain shadow of the Central Cordilleras (Ewel and Whitmore 1973). Annual rainfall is highly variable and averages 860 mm. August through November are generally the wettest months and December through March the driest. Temperatures fluctuate little throughout the year and average 25.1°C. Soils are generally shallow, alkaline, and derived from limestone rock (Lugo et al. 1978).

The 4500-ha protected area is a mosaic of forest stands with varying composition and structure arising from the interactions of topographic and edaphic features with land-use history (González-Liboy *et al.* 1976, Lugo *et al.* 1978, Murphy *et al.* 1995, Molina Colón and Lugo 2006, Agosto Diaz 2008). Parts of the forest were used for maize and goat production and a small settlement was located within its borders before the protected area was expanded in the 1930's. The forest was selectively cut for charcoal production extensively until the 1930's and in a limited amount until the 1970's, although this disturbance does not appear to have affected the composition or structure of the forest differently than hurricanes (Van Bloem et al. 2005, Molina Colón and Lugo 2006).

Gonzalez-Liboy et al. (1976) identified 6 major plant community associations (mangrove swamps, salt flats, beach associations, scrub forest, deciduous forest, and semi-evergreen forest) as well as two additional degraded associations (plantations and savanna) within Guánica Forest. They found the natural upland associations were largely demarcated by soil and leaf-litter thickness. The scrub forest was composed of widely spaced deciduous trees interspersed with shrubs and grasses. It was located on sites with thin soil and exposed limestone substrate that were found on the coastal slopes below 80 m above sea level, accounting for 29% of Guánica Forest. Deciduous forest had continuous and emergent canopy layers that opened in the dry season to allow grasses and shrubs to establish in the understory. It occupied sites with intermediate soil thickness, which accounted for 59% of the protected area. Semi-evergreen forest had a higher canopy and structural complexity than the deciduous and scrub forests. No grasses were noted in this association. It occupied sites with the deepest soils, generally in

saddles between ridges, about 7% of the protected area. Research for this thesis was conducted in deciduous and scrub forest areas.

Chapter 2
Fire resistance in a Caribbean dry forest: Inferences from bark characteristics

Introduction

A plant's response to wildfire depends on the degree to which it, along with its propagules, withstands or avoids burning. Plant life-history strategies for survival and reproduction in response to fire have been classified by Bond and van Wilgen (1996). Within this framework, Tropical dry forest (TDF) tree species have been classified into the following categories: recruiter, resprouter, resister, and vulnerable (Otterstrom and Schwartz 2006).

Recruiter refers to plants with high mortality in fire, but increased post-fire seed germination. These are generally short-lived plants with populations that fluctuate in rhythm with fire intervals. Heat and smoke induce seed germination.

Resprouter refers to plants that are able to survive fires by sprouting from the base and/or roots despite complete, or nearly complete, aboveground mortality (top-kill). This trait is associated with a variety of selective forces and is found under a wide range of fire regimes (Bond and van Wilgen 1996). Caribbean dry forest trees resprout vigorously in response to mechanical cutting (Ewel 1977, Murphy and Lugo 1986b, Murphy et al. 1995, McLaren and McDonald 2003a), hurricane-caused structural damage (Lugo et al. 1983, Whigham et al. 1991) and bending (Van Bloem et al. 2003, 2005, 2006). The adaptation for resprouting is likely associated with resilience to hurricane-force winds, but it may also increase survival in wildfires. When subjected to fires, tree species with the ability to resprout from belowground have higher survival than those that are limited to sprouting at or above the root collar (Saha and Howe 2003). Caribbean dry forest species generally resprout from above the root collar in response to hurricane winds (Van Bloem et al. 2003). Their post-fire sprouting ability apparently varies among species and decreases with repeated burning; however, a robust assessment is lacking (Santiago-García et al. 2008).

Resister describes plants that are able to maintain living organs aboveground through low- to medium-intensity wildfires. In trees, this capacity is provided by rhytidome (i.e., outer bark, dead tissue outward from the last-formed periderm) that insulates stems from the radiant heat of wildfire flames (Vines 1968, Bond and van Wilgen 1996). Bark's insulating properties

are primarily determined by its thickness, which is exponentially related to the amount of time cambial tissues reach lethal temperatures when exposed to fire (Whelan 1995). Bark thickness generally increases with stem size and varies widely among species. Because of this relationship, young and small trees are generally the most vulnerable to top-kill in fire (Pinard and Huffman 1997, Hoffmann and Solbrig 2003). Trees that inhabit areas with frequent, low- to medium-intensity fires (e.g., savannas) often develop bark that is thick enough to prevent topkill as saplings and continues to thicken with increasing stem diameter (Bond and van Wilgen 1996). Trees that inhabit areas that very rarely burn (e.g., moist and wet tropical forests, gallery forests) generally have bark that thickens with increasing stem diameter as well; however, they often do not develop bark that is thick enough to prevent topkill in even the largest stems (Uhl and Kauffman 1990, Hoffmann et al. 2003).

Plants that suffer high mortality in wildfires and sustained decreases in post-fire population size are termed vulnerable. These plants generally occupy sites that rarely burn in otherwise fire-prone environments, such as along bodies of water. Forests that rarely burn, such as intact moist- and wet-forests, are composed mainly of vulnerable trees (Uhl and Kauffman 1990, Hoffmann et al. 2003). This is apparently because vulnerable trees are better able to compete for resources than those that allocate carbohydrates to bark, suppressed buds, and non-structural reserves (Hoffmann et al. 2003).

Vegetative structure plays a large role in determining fire regimes (Whelan 1995). Areas with well-aerated fine fuels and open expanses exposed to winds typically experience faster spreading, larger, and therefore more frequent fires (Freifelder et al. 1998). In Guánica Forest, deciduous forest is the most extensive forest type and is characterized by a continuous tree canopy that allows sparse grasses in the understory. This is consistent with tropical forests that burn infrequently. However, the scrub areas are characterized by widely spaced trees interspersed with expanses of grasses and shrubs (Lugo et al. 1978) that appear to be more structurally similar to fire-prone savannas found in continental tropical locations (e.g., Hoffman et al. 2003)

The bark characteristics of the trees of Puerto Rico have been described in general terms by Little and Wadsworth (1964) and Little, Woodbury, and Wadsworth (1974), yet the measurements required to test hypotheses related to their fire survival have not been reported. In this study, the thickness, water content, and specific gravity of the bark of common trees in the

dry forest zone of Puerto Rico were measured and compared to those of other forests with various fire regimes and known ability to resist top-kill. I tested for differences in bark thickness at the population, species, and community levels in the scrub forest and deciduous areas of Guánica Forest. These results are used to predict the areas' fire regimes, explain the community response to anthropogenically increased fire frequencies, and suggest tree species for use in reforesting fire-prone areas.

Methods

Study Site

For this study, areas within Guánica Forest near the coastal road Rt. 333 (5 – 30 m above sea level) were used for the scrub forest measurements and areas near the Fuerte Capron trail (125 – 150 m above sea level) were used for the deciduous forest measurements.

Study design and field measurements

A total of 26 tree species were used for this study. Species were selected based on their relative abundances in the sampling plots of Lugo *et al.* (1978). The 11 tree species they encountered in their 10 x 100-m scrub forest plot and the 19 most common of 27 species in their two deciduous plots (each 10 x 100-m) were selected for measurements. Eight species were shared between the two forest types. *Pilocereus royenii* (ranked 7th in the scrub forest and 4th in the deciduous forest) was removed from the list because it is a cactus with a succulent stem that lacks a rhytidome. *Comocladia dodonea* (ranked 15th in the deciduous forest) was removed from the list because contact with the bark of this plant is extremely irritating to the skin. *Randia aculeata* (ranked 16th in the deciduous forest) was not measured because of difficulty locating and indentifying individuals. Seven additional tree species that were not encountered in the Lugo *et al*. (1978) plots were measured in this study to compare bark characteristics with sapling survival in a controlled burn experiment (Chapter 4).

Field and lab measurements were made between October and December 2008. Individuals to be measured were selected haphazardly by walking within the study area while searching for 5 stems of each species in each of 3 size classes (2.5-4.9, 5.0-10, and >10 cm diameter at 50 cm height) in both the scrub and deciduous forests. This sampling technique expedited measurements and closely approximated a stratified-random sample. Only one stem,

usually the largest, was measured on multi-stemmed trees. Stems with exterior necrosis or fungi were excluded from measurements. In total, 474 stems of the 26 selected species were measured. Size-class parameters were not fully met because of the rarity or absence of the larger size classes of some species in one or both of the forest types. Because large areas were extensively searched for trees in all size classes, the sample likely included individuals of each species near the maximum size that they generally obtain in both the deciduous and scrub areas of Guánica Forest. Excepted from this assumption was *Citharexylum fruticosum*, for which only two healthy-looking trees were encountered, both less than 5 cm stem diameter. For this reason *C. fruticosum* was excluded from analyses of bark thickness but included for bark specific gravity and water content.

Bark thickness was measured to the nearest 0.1 mm with calipers on an 11.1 mm diameter core that was extracted with a hollow steel punch from the north side of each stem at 50 cm height. A Suunto bark gauge was also used to measure bark thickness on a subset of stems, but it was found to provide unreliable measurements, especially on thin-barked stems. Stem diameter was measured to the nearest 0.01 cm at 50 cm and breast height (DBH, 130 cm) using a nylon diameter tape. Tree height was measured to the nearest 0.1 m using an extendable height pole. A description of the outer surface of the bark was noted for each measured tree using the terminology of Junikka (1994). These notes were then compiled and summarized to characterize each species (Table 2.1).

A subsample of 2-7 bark cores of each species was used to measure water content and specific gravity. After measuring their thickness, the cores were placed in airtight plastic bags and transported to the laboratory. Their fresh weight was taken within 24 hours of collection and core volume was measured using water displacement. Cores were then oven dried at 70°C to constant weight. Moisture content was calculated as (fresh mass – dry mass)/dry mass * 100. Specific gravity of the bark was calculated as dry mass/volume.

Analysis

I assumed a priori that there were differences among species in the relationship between bark thickness and stem diameter. To test for differences in this relationship within species between the two habitat types (scrub and deciduous forest) I used an ANCOVA test with bark thickness as the dependent variable, habitat type as a categorical variable, and stem diameter as a

covariable. Because this test was repeated 25 times (once for each species), a p-value of 0.01 was used to be less liberal in distinguishing differences between the habitat types.

Hoffmann and Solbrig (2003) found that a bark thickness of 6.6 mm provided 50% survival for four tree species in low-intensity (flame length <2 m) controlled burns in Brazilian cerrado savannas. I used this bark thickness to test for differences among species in the minimum stem diameter at which their bark is resistant to low intensity fires. I used an ANCOVA model with stem diameter as the dependent variable, species as a categorical variable, and bark thickness as a covariable. Mean stem diameter was compared among species at 6.6 mm bark thickness. Tukey-Kramer posterior tests were used to separate significantly different means ($p < 0.05$). Type III sums of squares were used in all tests to account for uneven sample sizes.

Community-wide trends in bark characteristics were compared between the scrub and deciduous forest with an index of relative importance that was calculated from the plot data of Lugo et al. (1978). For the 19 species that were encountered in their plots and measured in this study, an importance value (IV) was calculated as the sum of relative stem density and relative basal area in each plot. These values were then averaged for the two deciduous forest plots. Each species' relative importance was taken as (Scrub Forest IV +1)/(Deciduous Forest IV +1). One was added to the IV values to prevent values of zero and infinity. This calculation was adapted from Engelbrecht et al. (2007). To determine if species with thicker bark had higher relative importance in the scrub forest, the calculated IV values were plotted against the relative stem size with 6.6-mm bark (stem diameter with 6.6-mm bark divided by species maximum stem diameter).

Results

Bark thickness generally increased with stem diameter and varied widely among species (Figure 2.1). Twenty of the species had significant regression coefficients, while five did not (Table 2.3). The species that did not have significant regression coefficients were measured over only a small range of stem diameters because their maximum stem size was low (Figure 2.1).

The ANCOVA model showed that the bark thickness x stem diameter interaction was significantly different between habitat types for five species. Four of these had bark thickness that increased more steeply with stem diameter in the scrub forest (*A. elemifera, B. succulenta*, *C. cynophallophora*, and *T. portoricensis)*. One species had bark thickness that increased more

steeply in the deciduous forest (*T. heterophylla)*. Most of these significant differences were apparently the result of one or two outlying trees rather than clear differences in bark thickness between habitat types. These results suggest that tree species do not vary in their bark thickness between scrub and deciduous forest habitats.

Nine of the 25 species that were measured across their effective size ranges never obtained bark with 6.6 mm thickness – the minimum thickness that Hoffmann and Solbrig (2003) estimated as sufficient to provide 50% survival in low-intensity fires. The remaining 16 species were tested for differences among species in their stem size at which their bark reached this criterion. The interaction term was significant in the model, indicating that the bark thickness x diameter regression slope varied among species; however, variable regression slopes do not invalidate point comparisons of least-squared means. Tree species reached 6.6 mm bark thickness at stem diameters ranging from 7.2 to 23.0 cm (Table 2.3). These values ranged from 31 to 127% of the diameter of the largest size tree measured within each species. Based on the size at which their bark obtained fire resistance relative to their maximum size, the tree species could be placed in the following groups: never reaching fire resistance (n = 9 species), only large-sized stems (>50 % of the maximum stem size) obtain fire resistance (n = 14 species), small-sized stems (<50 % of the maximum stem size) obtain fire resistance (n = 2 species; Table 2.3).

Tree species showed a wide range of relative importance values between the scrub and deciduous forests, but most species had values near 1, indicating little evidence for habitat preference or filtering between the scrub and deciduous forests (Table 2.1). Tree species that never obtained fire-resistant bark thickness and those that obtained it only in relatively large stems showed no trends in importance between the scrub and deciduous forests, while the two species that obtained fire-resistant bark in relatively small stems were highly over represented in the scrub forest (Figure 2.2). This trend held when analyzed with relative basal diameter and stem density (not presented).

Bark water content and specific gravity ranged 50.3 – 265.9% and 0.29 – 0.79 $g \cdot cm^{-2}$ (Table 2.2). Both attributes varied significantly among species. The two attributes were correlated (Pearson $r^2 = -0.68$, $n = 26$, $p < 0.001$), but no relationship was found among them and bark thickness. The ranges of these values were within those obtained by Pinard and Huffman (1997), who found that the insulating effect of bark were not influenced by its water content or

specific gravity. This observation strengthens the premise for using bark thickness as the focus of evaluating fire-resistance without direct measurements of fire-performance.

Discussion

Most trees in Guánica Forest had bark that is unlikely to prevent top-kill in low-intensity fires. While some species obtained bark that was thick enough to prevent top-kill, most of these species only obtained it on relatively large trees (minimum stem diameters of 7.2 to 23.0 cm). Trees that grew in the gallery forest of the Brazilian cerrado obtained low-intensity fire-resistant bark at similar stem diameters (7.0 to 20.3 cm, 10 species), whereas congeners that grew in nearby fire-prone savannas obtained comparable bark thickness at stem diameters between 3.1 and 6.0 cm (Hoffmann et al. 2003). The early onset of fire-resistant bark in the savanna tree species was attributed to an adaptation in response to the frequent occurrence of fire. In these trees resources were allocated to bark growth at the expense of growth in other areas (Hoffmann et al. 2003). The trees of Guánica Forest did not show this characteristic; instead their bark resembled that of the Brazilian gallery forests where fires were uncommon. Similarly, trees in hardwood forests of Illinois obtained bark of this thickness at stem diameters of 7.2 to 21.4 cm (15 species; calculated with regression equations. *Quercus rubra* excluded here because it was projected to have 6.6 mm bark at a negative stem diameter) (Hengst and Dawson 1994).

Trees in the Amazon have very thin bark, averaging just 7.1 mm (SE = .14 mm) on trees >20 cm DBH (Uhl and Kauffman 1990). Likewise, trees in the Amazon that were <10 cm DBH had bark that ranged 0.7 to 3.2 mm and trees 10 to 20 cm DBH had bark that ranged 1.0 to 9.5 mm (Uhl and Kauffman 1990). Trees in these size classes in Guánica Forest had bark with higher-ranging thicknesses, 0.6 to 9.5 mm and 2.3 to 16.8 mm respectively. Much like trees in Guánica Forest, those in the Amazon acquire low-intensity fire-resistant bark only in some species and for those only in large trees (Uhl and Kauffman 1990). The major difference between the two forests is their structure. Uhl and Kauffmann (1990) calculated that trees >20 cm DBH accounted for 56.9 % of the basal area in their Amazonian plots while trees rarely reach this size in Guánica Forest (0.05% of stems in Muphy and Lugo 1986b).

Tree size is limited in Guánica Forest by persistent soil water deficits, occasional hurricane-force winds, and the selective cutting that occurred before the 1950's (Lugo et al. 1978, Murphy and Lugo 1986b, Van Bloem et al. 2005). The small size of most trees in the

forest increases their vulnerability to fire. In the deciduous forest, only about 5% of stems (DBH >2.5 cm) had DBH >7.5 cm, whereas about 80% were <5 cm DBH (Murphy and Lugo 1986b). As trees acquire fire resistant bark at 7.7 to 23 cm diameter, at least *ca.* 95% of the stems in the deciduous forest are vulnerable to low-intensity fire (Figure 2.3).

The scrub forest is characterized by a lower density of intermediate-sized stems than the deciduous forest (540 versus 1750 stems·ha^{-1} >5 cm DBH), but about equal density of larger stems (140 versus 135 stems·ha^{-1} >10 cm DBH) (Lugo et al. 1978). So a lower percentage of stems in the scrub forest are vulnerable to fire. Soils in the scrub areas of Guánica Forest are very thin and rock outcroppings are common (Lugo et al. 1978). These landscape features may act as firebreaks that protect trees from fires, permitting them to persist in fire-prone areas (Clarke 2002). My casual observations suggested that large trees in the scrub areas of Guánica Forest generally occupy sites that are surrounded by rocky outcrops. Although a detailed inventory is lacking, it is possible that the increased relative importance of large sized trees in the scrub forest is a result of past fires that killed small stems but left protected stems.

The trees of Guánica Forest have extremely slow growth rates (S. J. Van Bloem, unpublished data). For example, *B. buceras* DBH grew on average 0.06 and 0.13 cm·yr^{-1} in two long-term studies in Guánica Forest (Lugo 1983). At these rates it would take 117 to 253 years for this species to reach the 15.2 cm minimum diameter size with bark that is sufficiently thick to survive a low-intensity fire. Hoffmann and Solbrig (2003) estimated that a bark thickness of 11.4 mm was the minimum sufficient to provide 50% tree survival in high-intensity fires (>2 m flame length). Only two of the sampled species obtained bark this thick – *B. simaruba* and *T. heterophylla.* While *B. simaruba* consistently obtained bark this thickness at stem diameters >19 cm, only a single individual of *T. heterophylla* was measured with bark >11.4 mm thick (Figure 1). In another study, Pinard and Huffman (1997) estimated that bark ≥18 mm thick was necessary to prevent lethal cambial temperatures in low-intensity experimental burns in a Bolivian tropical dry forest. Only two individuals measured in Guánica Forest had bark that reached this threshold – *B. simaruba* of 23.3 and 30.6 cm diameter.

B. simaruba stood out as the most fire-resistant species that was sampled in this study. Although some other species acquired bark thickness at a similar rate relative to stem diameter, their stems reached their maximum size before the bark reached a thickness able to withstand high-intensity fires. Only *B. simaruba* continued to put on thick bark into the larger stem

diameters able to withstand high-intensity fires. Ewel and Whitmore (1973) described *B. simaruba* as a fire-tolerant species that grew as large, isolated trees in annually burned grasslands. Gleason and Cook (1927) noted that *B. buceras* did this as well. It is possible that the large individuals of these two species, which constitute the majority of the basal area of the scrub forest in Guánica Forest, are survivors of past fires that removed other species from the area. With the present data it is difficult to know to what extent past fires have affected the scrub forest. However, it is clear that a single low-intensity fire has the potential to top-kill the vast majority of trees in Guánica Forest. More frequent fires would exclude all but the largest size classes of a few species.

Table 2.1 List of species that were measured in this study. Scr./Dec. Relative IV is the relative importance value between scrub and deciduous habitats in Guánica Forest. See text for how this was calculated. Range information is from Little and Wadsworth (1964) and Little, Woodbury, and Wadsworth (1974).

Family	Species	Scr./Dec. Relative IV	Range
Rutaceae	*Amyris elemifera* L.	1.00	Florida, Guatemala, El Salvador, Honduras, Caribbean
Boraginaceae	*Bourreria succulenta* Jacq.	0.90	Caribbean islands, Panama to Venezuela
Combretaceae	*Bucida buceras* L.	1.75	Florida Keys, Caribbean Islands, Mexico to Guianas
Burseraceae	*Bursera simaruba* (L.) Sarg.	1.53	Florida, Mexico to Guiana, Caribbean
Capparaceae	*Capparis hastata* Jacq.	0.98	Caribbean islands, Venezuela, Colombia
Capparaceae	*Capparis cynophallophora* L.	0.99	Southern Florida, Caribbean, Mexico to Panama
Verbenaceae	*Citharexylum fruticosum* L.	.	Florida, Caribbean, Venezuela to Suriname
Polygonaceae	*Coccoloba diversifolia* Jacq.	.	Florida, Caribbean Islands
Polygonaceae	*Coccoloba microstachya* Willd.	1.09	Puerto Rico, Hispaniola, Virgin islands
Polygonaceae	*Coccoloba uvifera* (L.) L.	.	Widely distributed on tropical American shores
Celastraceae	*Crossopetalum rhacoma* Crantz	.	Southern Florida, Caribbean Islands, Mexico, Honduras, Venezuela
Erythroxylaceae	*Erythroxylum areolatum* L.	0.99	Caribbean Islands, Southern Mexico to Honduras
Rubiaceae	*Exostema caribaeum* (Jacq.) Roem & Schult.	0.63	Florida, Mexico to Costa Rica, Caribbean
Zygophyllaceae	*Guaiacum officinale* L.	0.98	Caribbean Islands, Panama to Guiana
Rubiaceae	*Guettarda elliptica* Sw.	.	Southern Florida, Caribbean, Mexico to Guiana
Euphorbiaceae	*Gymnanthes lucida* Sw.	1.02	Southern Florida, Caribbean, Mexico to Honduras
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urban	0.95	Southern Florida, Caribbean, Mexico to Honduras
Leguminosae	*Leucaena leucocephala* (Lam.) de Wit	.	Caribbean Islands, Mexico to South America
Leguminosae	*Pictetia aculeata* (Vahl) Urban	0.98	Puerto Rico, Virgin Islands, Hispaniola
Nyctaginaceae	*Pisonia albida* (Heimerl) Britton, ex Standl.	0.67	Hispaniola, Puerto Rico, Mona, Caja de Muertos
Leguminosae	*Pithecellobium unguis-cati* (L.) Benth.	0.97	Southern Florida, Caribbean, Mexico to Guiana
Apocynaceae	*Plumeria alba* L.	1.10	Caribbean islands
Rhamnaceae	*Reynosia uncinata* Urban	1.09	Caribbean islands
Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	.	Caribbean islands
Sapindaceae	*Thouinia portoricensis* Radlk.	0.97	Puerto Rico
Rutaceae	*Zanthoxylum flavum* Vahl	0.96	Southern Florida, Caribbean

Table 2.2. Form and bark texture for the 26 species measured in this study. Form descriptions are from Little and Wadsworth (1964) and Little, Woodbury, and Wadsworth (1974). Bark texture descriptions are from field notes.

Species	**Form**	**Bark Texture**
A. elemifera	small tree or shrub	Rugose with shallow fissures that become deep on largest trees
B. succulenta	small tree or shrub	Soft, fibrous, sometimes with shallow fissures and/or scaly patches
B. buceras	medium-sized to large spreading tree	Shallow fissures, scales common near base, sometimes lenticels
B. simaruba	medium-sized tree, spreading	Smooth with papery scales, sometimes lenticels
C. cynophallophora	small tree or shrub, small to medium tree	Rugose, often has burls, sometimes hoops
C. hastata	small tree or shrub	Rugose, sometimes with lenticels and shallow fissures
C. fruticosum	shrub or small slender tree	Fibrous, shallow fissures
C. diversifolia	usually small tree	Heterogeneous, rugose, irregular scales and/or flakes
C. microstachya	shrub or small tree	Tessellated, sometimes heterogeneous with smooth, lenticellate sections
C. uvifera	small tree or shrub	Rugose, some scales and lenticels
C. rhacoma	shrub, sometimes small tree	Close, small scales or shallow fissures
E. areolatum	small tree or shrub	Close, small scales or rugose
E. caribaeum	shrub or small tree	Smooth with lenticels. Larger stems sometimes have deep v-shape fissures
G. officinale	small tree	Patchy, irregular scales; sometimes slab-like flakes
G. elliptica	shrub or small tree	Rugose, sometimes patches of irregular scales
G. lucida	small tree or shrub	Rugose, lenticels, sometimes scales or flakes
K. ferreum	small tree or shrub	Long, v-shape fissures with hollow ridges
L. leucocephala	small tree or shrub, spreading	Rough, sometimes with shallow fissures and lenticels arranged in vertical lines
P. aculeata	small tree, tree or shrub	Smooth with lenticels; shaggy flakes on larger trees
P. albida	usually small tree, spreading	Rugose with lenticels, sometimes shallow fissures and scales on large trees
P. unguis-cati	shrub or small tree	Smooth or rugose with paired prickles
P. alba	small tree or shrub	Smooth or rugose, sometimes with lenticels, shallow fissures, and/or scales
R. uncinata	shrub or small tree	Shallow fissures, scales
T. heterophylla	small to medium sized tree	Long, shallow fissures, sometimes deep on larger trees
T. portoricensis	small tree or shrub	Adherent scales
Z. flavum	small to medium sized tree	Shallow, reticulate fissures

Table 2.3. Bark thickness as a function of stem diameter, specific gravity, and percent water content for 26 species in Guánica Forest. n Dec and n Scr are the sample sizes in the scrub and deciduous forests. Mean (SE) slope and intercept values are from simple regressions of stem diameter on bark thickness. * p<.05, **p<.01, ***p<.001 for Slope. Minimum fire-resistant diameter (Min. F.R. diam.) is the stem diameter with 6.6 mm bark. See text for how this was calculated. Max diam. is the diameter at 50 cm height of the largest stem. Final column is sample size used to calculate mean and (SE) of specific gravity and percent water content. Means that share a letter are not significantly different using a Tukey-Kramer test (p < 0.05).

Species	n Dec	n Scr	Intercept	Slope		Min F.R. Diam.	Max Diam.	Specific Gravity ($g\ cm^{-3}$)		Percent Water Content		n
A. elemifera	12	12	0.99 (0.55)	0.42 (0.08)	***	9.93	12.65	0.65 (0.04)	ABCD	70.2 (2.3)	EFGHI	5
B. succulenta	17	7	1.85 (0.20)	0.08 (0.03)	*	18.24	14.31	0.44 (0.04)	CDE	117.1 (10.4)	BCDEF	5
B. buceras	17	17	2.42 (0.39)	0.24 (0.03)	***	15.20	30.70	0.62 (0.06)	ABCD	84.2 (5.8)	DEFGHI	6
B. simaruba	16	18	2.11 (0.41)	0.56 (0.03)	***	9.62	30.61	0.29 (0.02)	E	265.9 (14.6)	A	6
C. cynophallophora	4	11	0.35 (0.47)	0.41 (0.06)	***	13.56	16.00	0.69 (0.03)	ABCD	62.2 (3.9)	EFGHI	5
C. hastata	6	0	0.93 (0.63)	0.30 (0.11)		-	8.49	0.63 (0.08)	ABC	74.4 (6.7)	GHI	5
C. fruticosum	0	2	-	-		-	-	0.35 (0.00)	DE	50.3 (1.1)	FGHI	2
C. diversifolia	11	2	1.08 (0.48)	0.16 (0.09)		-	7.30	0.54 (0.08)	ABCD	107.9 (11.3)	BCDEFG	5
C. microstachya	10	10	-0.15 (0.41)	0.65 (0.07)	***	9.42	8.90	0.49 (0.03)	BCDE	52.8 (5.4)	I	5
C. uvifera	0	9	1.04 (0.16)	0.24 (0.02)	***	-	19.35	0.41 (0.04)	DE	147.8 (9.5)	BC	5
C. rhacoma	8	5	1.01 (0.16)	0.11 (0.03)	**	-	9.91	0.66 (0.07)	ABCD	52.0 (5.2)	I	5
E. areolatum	8	9	2.55 (0.40)	0.29 (0.05)	***	12.01	16.40	0.49 (0.01)	BCDE	128.5 (6.6)	BCD	5
E. caribaeum	15	13	1.22 (0.43)	0.37 (0.06)	***	11.22	15.80	0.58 (0.03)	ABCD	89.0 (8.2)	DEFGHI	5
G. officinale	4	11	2.02 (0.64)	0.23 (0.06)	**	14.81	16.60	0.79 (0.01)	A	55.2 (2.6)	HI	5
G. elliptica	8	10	0.06 (0.91)	0.30 (0.22)		-	6.80	0.71 (0.07)	AB	80.8 (13.9)	DEFGHI	6
G. lucida	8	10	1.37 (0.23)	0.08 (0.04)		-	9.04	0.59 (0.04)	ABCD	98.7 (3.7)	CDEFGHI	6
K. ferreum	13	12	1.26 (0.43)	0.47 (0.06)	***	9.91	13.42	0.69 (0.04)	AB	67.4 (3.1)	GHI	7
L. leucocephala	8	11	1.86 (0.27)	0.36 (0.05)	***	11.33	12.41	0.55 (0.03)	ABCD	94.9 (5.8)	DEFGHI	6
P. aculeata	13	19	1.99 (0.30)	0.20 (0.03)	***	14.06	23.00	0.66 (0.03)	ABCD	73.0 (14.0)	EFGHI	5
P. albida	16	15	0.97 (0.27)	0.18 (0.03)	***	22.96	23.95	0.41 (0.04)	DE	121.7 (14.1)	BCDE	5
P. unguis-cati	6	8	0.60 (0.53)	0.52 (0.11)	***	-	7.70	0.59 (0.06)	ABCD	105.0 (5.2)	BCDEFGH	5
P. alba	7	11	0.70 (0.75)	0.77 (0.12)	***	7.19	11.20	0.44 (0.02)	CDE	159.0 (19.6)	B	4
R. uncinata	2	8	2.05 (0.29)	0.15 (0.06)	*	-	10.22	0.64 (0.06)	ABCD	72.2 (15.9)	DEFGHI	3
T. heterophylla	8	8	1.68 (0.86)	0.44 (0.09)	***	10.00	17.30	0.60 (0.05)	ABCD	85.6 (9.4)	DEFGHI	6
T. portoricensis	10	6	0.88 (0.64)	0.25 (0.15)		-	6.00	0.44 (0.04)	CDE	109.6 (15.0)	BCDEFGH	4
Z. flavum	6	2	2.16 (0.78)	0.23 (0.08)	*	15.36	16.06	0.63 (0.04)	ABCD	81.7 (11.9)	DEFGHI	5

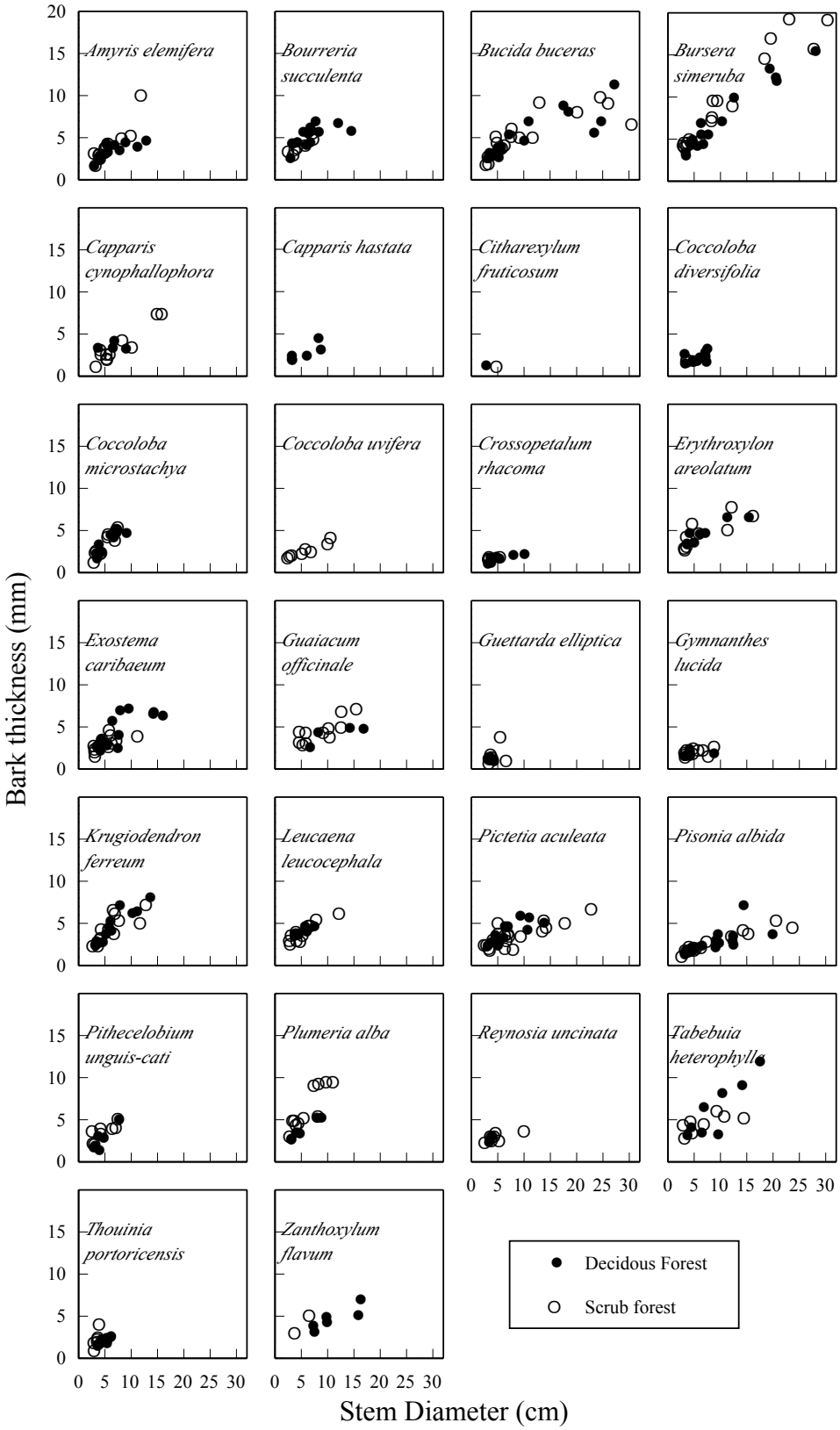

Figure 2.1. Stem diameter and bark thickness of all trees measured in this study.

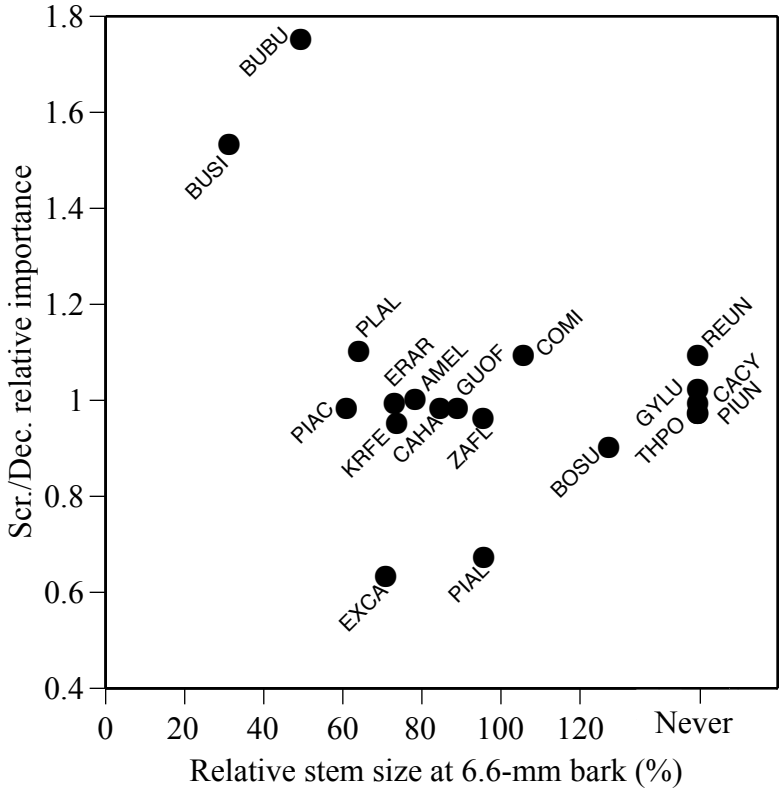

Figure 2.2 Species relative stem size at 6.6-mm thick bark versus relative importance between the scrub and deciduous forest plots of Lugo et al. (1978). See text for how these values were calculated. Labels are the first two letters of the genus and species.

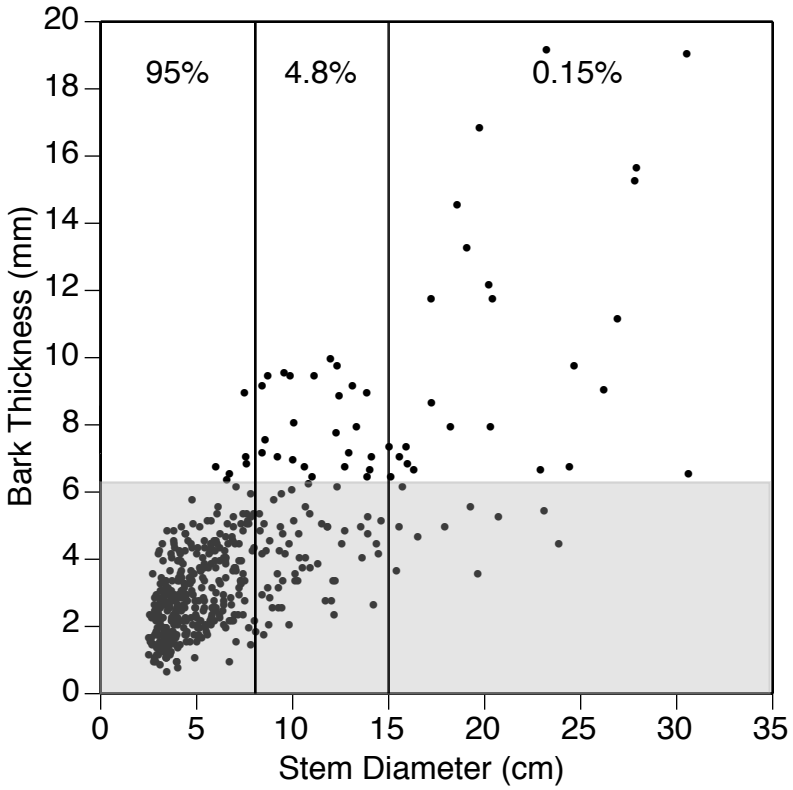

Figure 2.3. Stem diameter and bark thickness of all trees measured in this study. Trees within the shaded area have bark thickness <6.6 mm, making them vulnerable to low-intensity wildfires (See Hoffmann and Solbrig 2003). Vertical lines and percentages show the size-class structure of a deciduous forest plot in Guánica Forest (Murphy and Lugo 1986b). Medium and large size classes were overrepresented in this study to assess bark thickness across each species' size range. A random sample of 474 stems would contain on average 450 stems <7.5 cm DBH, 23 stems 7.5-15 cm DBH, and 1 stem >15 cm DBH.

Chapter 3

Patterns of seed rain in Caribbean dry forest degraded by agriculture and fire

Introduction

In the dry forest zone of southwest Puerto Rico, the exotic tree species *Leucaena leucocephala* (Lam.) de Wit (Fabaceae-Mimosoideae) dominates secondary forest stands for >50 years after land abandonment (Molina Colón and Lugo 2006, Pérez Martínez 2007). Degraded areas in this zone are also dominated by exotic forage grasses (e.g., *Pennisetum ciliare* (L.) Link *Bothriochloa pertusa*, (L.) A. Camus., and *Urochloa maxima* (Jacq.) R.D. Webster) that are maintained as grassland-savannas by anthropogenic fires (Ewel and Whitmore 1973, Francis and Parrotta 2006). Persistent exotic plant communities in degraded areas indicate a failure of native plants to establish there, but exotic forests may enhance native tree recruitment by ameliorating soils, suppressing grasses, and increasing seed input (Parrotta et al. 1997, Lugo and Helmer 2004). Caribbean dry forests generally have depauperate seedbanks (Castilleja 1991, Ray and Brown 1994, Murphy et al. 1995), so forest regeneration in areas cleared of rootstocks, either mechanically or through burning, is largely dependant on propagule input from outside the disturbed area. As such, seed input is the primary factor that limits forest recovery, while factors such as seed predation, seed germination, and seedling survival and growth act subsequently to determine successional plant communities (Holl et al. 2000).

Dispersal limitation, defined as the failure of seeds to arrive at all sites suitable for recruitment, has been shown to contribute to species diversity in tropical forests by slowing competitive exclusion (Dalling et al. 2002). It has also been shown to limit tree density and diversity in successional fields because few seeds arrive to areas beyond forest edges (Holl 1999, Wijdeven and Kuzee 2000)

Most studies of seed dispersal in degraded tropical forests have focused on abandoned cattle pastures (e.g., Duncan and Chapman 1999, Holl 1999, Wijdeven and Kuzee 2000, Dosch et al. 2007, Zamora and Montagnini 2007). Patterns of seed rain in burned TDF could be expected to follow those of abandoned pastures because of their similar vegetation and spatial attributes (i.e., large expanses of grasses), although burned areas are generally more heterogeneous than cattle pastures. Pastures adjacent to forests have straight edges for borders, while fires burn in irregular patterns determined by fuel loads, topography, and weather conditions (Whelan 1995). Isolated trees in pastures have strong effects on seed rain density and

composition, particularly for animal-dispersed seeds (McDonnell and Stiles 1983, Slocum and Horvitz 2000). Fires often leave isolated patches of vegetation in their wake that could act as seed sources and attract seed dispersers. Early colonizing trees increase the structural complexity of grasslands and attract birds and bats because they act as perches and forage locations (Wunderle 1997). However, early colonizing trees may slow the input of ballistic and wind-dispersed seeds because they physically block their movement and reduce surface lift that carries these seeds long distances (Nathan and Katul 2005).

In order to better understand how *L. leucocephala* comes to dominate successional dry forest areas and how this dominance affects the capacity for native tree species to regenerate in these areas, I collected seed rain along a gradient of vegetative degradation in four sites across Guánica Forest. With these data I tested the following hypotheses:

1. In the absence of fire, open grassland areas become dominated by *L. leucocephala* trees because their seed input outnumbers that of native trees.
2. Exotic forests facilitate native tree regeneration by increasing the input of zoochoric tree seeds compared to open grasslands.

Methods

Study Site

Four areas of Guánica Forest were selected for this study based on their local disturbance histories (M. Canals, personal communication), which resulted in the close proximity of stand-level patches with varying degrees of degradation of the plant composition. The areas were spread throughout the forest, but three of the four sites were located near its borders, where the majority of fires have occurred (Figure 3.1). Three of these sites experienced isolated fires 1 to 25 years prior to seed trapping and the fourth site was bulldozed *ca*. 20 years prior to trapping (Table 3.1). The sites varied in topography, soil characteristics, and distance from the coast. Within each trapping site, five vegetation types were identified based on the dominance of exotic or native species in the composition of canopy trees and the presence or absence of exotic grasses in the understory: open exotic grasslands, exotic forests with exotic grassy understories, exotic forests with woody understories, native forests with exotic grassy understories, and native forests with woody understories.

Experimental design and field measurements

Seed traps were constructed of 0.5 x 0.5 m frames that were fitted with 1-mm mesh baskets and suspended 40 cm above the ground with PVC plastic tubing legs. This seed trap design has been shown to reliably estimate seed rain with minimal fruit loss due to wind, predation, or bouncing (Stevenson and Vargas 2008). A height of 40 cm was chosen to conceal the traps within the grass and understory shrubs so as to prevent vandalism and bird perching, which could bias results. Vegetation, usually grass or vines, growing within or directly upon the traps was cleared away monthly. Twenty-five traps were placed at each of the four sites in random locations such that they were at least 20 m away from each other, five in each of the five vegetation types. Randomization was introduced after locating areas with the focal vegetation types by sequentially placing each trap at a distance (20 - 60 m) and direction determined by the second hand on a watch. As the vegetation was heterogeneous within the stands, traps had varying degrees of *L. leucocephala* and grass in their vicinity (Table 3.1). Seeds were collected from the traps monthly from July 2007 to June 2008 and brought to the laboratory where they were air dried if needed and stored in paper envelopes in an air-conditioned room until they were sorted and counted 92 ± 28 days later (mean ± SD). Seeds were identified by comparison with field-collected samples and those of the UPRM herbarium. The 10 trees (> 2.5 cm diameter at 130 cm height) nearest to each trap were mapped and monitored for the presence of fruits and flowers during each monthly seed collection.

The understory plant community around each seed trap was measured in September 2008. Three 0.5 x 0.5 m plots were located 1 m from each trap in randomly selected, perpendicular directions. Within each plot the grass cover was visually estimated to the nearest 5% and grass crowns were counted and identified to species (crowns connected by stolons or rhizomes were counted as separate individuals). Woody plants (shrubs, lianas, and trees) <2.5 cm dbh were counted and categorized by species and height classes of <30 cm, 30 – 100 cm, and >100 cm.

Data analysis

Seed counts for the 12 monthly collections were added for each species within each trap and species were classified according to their dispersal syndrome based on morphological characteristics as described by Castilleja (1991) and Little and Wadsworth (1964) for trees and

Acevedo-Rodríguez (2003) for vines. Only counts of tree seeds were included in the statistical analyses, as tree regeneration was the focus of this study. Native tree seeds were grouped as animal- or abiotically-dispersed. *Prosopis pallida* was the only exotic tree species other than *L. leucocephala* with seeds that were collected and indentified in the traps. This species was included with the animal-dispersed species. *Bucida buceras* seeds have no apparent dispersal syndrome (Castilleja 1991) and although they have been circumstantially reported to be dispersed by pigeons (Amadeo 1888), I observed no evidence that they were dispersed by anything other than wind or gravity. This species was classified as abiotically dispersed for analyses. The number of seeds that arrived to each trap was highly skewed because many traps received no seeds of a particular type and a few received thousands, which is typical for seed rain data (Dalling et al. 2002). Therefore, generalized linear models (GLIM) with negative binomial distributions and log-likelihood functions were used to compare mean seed counts. These analyses were run using proc GLIMMIX in SAS 9.1 (SAS Institute, Inc. Cary, North Carolina).

The hypothesis that *L. leucocephala* seeds fall at higher rates than native seeds in open grass areas was tested with the counts from the 25 traps that were placed in grassy areas. Counts were modeled with seed type and site as main factors. Their interaction was included in the model as well as a trap effect, which was nested within site (two factor split-plot design).

To test the second hypothesis, that exotic forests receive higher inputs of native tree seeds than open grasslands, the counts of the three seed types (animal-dispersed, abiotically-dispersed, and *L. leucocephala*) were each tested separately in a model that included site, vegetation type, and their interaction as factors (two factor design). This model was also applied to counts that excluded seeds from the tree species that were present in the 10 trees nearest to each trap or had part of their crown covering the trap. As trees generally disperse the majority of their seeds below their own crown (Dalling et al. 2002), this test was used to verify that the encountered patterns of seed rain were not simply an effect of the seeds falling directly from the crowns covering each trap, but rather of being dispersed from sources other than trees surrounding the trap. It is a conservative test because seeds that were dispersed from a distance outside the 10 nearest trees were excluded if they were from a species within the 10 nearest trees. One trap was excluded from this analysis because its nearest trees were not recorded.

Results

The traps collected a total of 35,610 non-graminoid seeds from July 2007 to June 2008, of which 34,922 (98%) were identified to family, 34,880 to genera, and 34,281 to species (Table 3.2). Tree seeds accounted for 80.3% of the total, vines 15.5%, shrubs and forbs 1.5%, and epiphytes 0.5%. A total of 48 species and morphospecies were identified; 30 trees, 8 vines, 5 shrubs and herbs, and 1 epiphyte (Table 3.2). *L. leucocephala* was the most abundant species, with 11,582 seeds. *Pisonia albida* was the most abundant native species, with 7065 seeds, of which 7055 were collected in two traps.

Do open grass areas receive more L. leucocephala *seeds than native trees seeds?*

Overall the seed rain in open grass areas was low. A total of 637 tree seeds were collected in these areas, 457 of which were *L. leucocephala* and 180 were native tree seeds. Only one animal-dispersed tree seed was collected in the open grass areas, the rest were wind-dispersed or ballistic (Table 3.2). Six of the 25 traps did not collect any tree seeds and the most tree seeds collected in a trap was 144. The mean count of each seed type was <0.1 per trap. In the GLIM model of seed rain, the effects of seed type, site, seed type x site, and trap were not significant factors (Appendix A). Thus, no difference in seed input was detected among *L. leucocephala,* animal-dispersed, and abiotically-dispersed seeds in grassy areas at any of the sites. The sites did not vary in the model either; however, this may reflect more an inability to statistically detect differences among the sites than an actual lack of difference. The open grass traps at La Hoya received a mean of 26.8 ± 10.4 seeds of each type while the other sites had means that were essentially zero.

Do exotic forests have increased seed fall of native trees compared to open grass areas?

The traps in exotic forest vegetation (woody and grassy understory combined) collected 11,406 tree seeds, of which 10,763 were *L. leucocephala* and 643 were from other species. Thirteen of the 17 animal-dispersed tree species were collected in the exotic forest traps, totaling 458 seeds. Seven of the 12 abiotically-dispersed tree species were collected there, totaling 185 seeds.

The GLIM models of animal- and abiotically-dispersed seed rain showed contrasting patterns between the two seed types and among the five vegetation types. The analysis of animal-

dispersed seeds showed vegetation type and the site x vegetation interaction as significant factors (Appendix A). Each site had a unique pattern of mean seed rain among the five vegetation types. At Cuevas and Pitirre native forests with woody understories had significantly higher seed rain than the other vegetation types while at Ensenada and La Hoya exotic forests received similar seed input (Figure 3.2a). At all four sites exotic forests had higher animal-dispersed seed rain than open grass areas, which was zero at three of the open-grass sites (Figure 3.2a).

For abiotically-dispersed seeds the GLIM model showed vegetation type, site, and the vegetation type x site interaction as significant factors. As with animal-dispersed seeds, each site had a unique pattern of seed rain among the five vegetation types and native forests tended to have higher seed inputs than the other vegetation types (Figure 3.2b.). However, unlike animal-dispersed seeds, there was no pattern of higher seed fall of abiotically-dispersed seeds in exotic forests compared to open grass. At Cuevas and La Hoya open grass traps collected more abiotically-dispersed seeds than exotic forests with woody understories and a similar number of seeds in exotic forests with grassy understories. At Ensenadas no abiotically-dispersed tree seeds were collected in the open grass while traps in the exotic forest with woody understory and exotic forest with grass understory had abiotically-dispersed tree seed rain densities of 6.4 ± 3.9 and 1.6 ± 1.4 m^{-2} (mean ± SE) respectively. At Pitirre no abiotically-dispersed tree seeds were collected in the exotic forest with grass understory while the exotic forest with woody understory and open grass traps received 4.0 ± 2.7 and 1.6 ± 1.4 seeds m^{-2} respectively.

When the seeds from tree species surrounding the traps were excluded from the total count, only 2106 (7.5%) tree seeds remained: 812 were animal-dispersed, 1147 were abiotically-dispersed, and 147 were *L. leucocephala.* This indicates that a large majority of the seeds collected were likely dispersed from within a few meters of the traps. The GLIM models showed that the general patterns observed in the total seed count remained despite the large reduction of seeds included in the analyses (Figure 3.3a-b). For animal-dispersed seeds the GLIM showed vegetation type as a significant factor while site and the site x vegetation type interaction were not (Apendix A). None of the open grass traps collected animal-dispersed tree seed from species that were outside its immediate vicinity. Traps in exotic forests with woody understories had means of animal-dispersed seeds from species outside their vicinity that ranged 1.6 – 41.6 seeds·m^{-2} and traps in exotic forests with grassy understories ranged from 0 – 5.6 seeds·m^{-2}. Traps in native forests with and without grassy understories tended to collect more animal-

dispersed seeds from species outside their vicinity than traps in exotic forests (range 0.8 – 406.4 seeds·m^{-2}; Figure 3.a). For abiotically-dispersed seeds the GLIM showed vegetation type and the site x vegetation type interaction as significant factors (Appendix A). The patterns of tree seed rain among vegetation types within sites remained essentially the same as those of the total count of abiotically-dispersed tree seed, except at La Hoya, where native forest traps had higher total seed counts than the other vegetation types but the counts of seeds from species outside the trap vicinity were similar in all vegetation types (Figure 3.3b).

Discussion

This study tracked seed rain in stands of various states of degradation across Guánica Forest. Few tree seeds arrived to open grass areas and no differences were found in the number of *L. leucocephala,* animal- and abiotically-dispersed seeds at any of the sites. This suggests that *L. leucocephala* and native trees are similarly dispersal-limited in open grass areas. Demographic factors other than seed dispersal may favor *L. leucocephala* recruitment when fires do not reoccur in these areas. Factors such as seed viability, longevity, predation, and germination as well as seedling tolerance of degraded soils, grass competition, and increased solar radiation may favor *L. leucocephala* recruitment in these areas.

A consistent pattern emerged that seed rain of animal-dispersed seeds increased in exotic forests compared to open grasslands. Only one animal-dispersed tree seed was collected in traps in the open grass sites, whereas 458 seeds of 13 animal-dispersed tree species were collected in exotic forest traps (woody and grass understory traps combined). When seed counts included only tree species not surrounding the traps, exotic forest traps still had 85 seeds of 12 animal-dispersed species. On the other hand, abiotically-dispersed seed rain in open grass traps was equal to or higher than in the exotic forest at three of the four sites. This suggests that exotic forests attract seed dispersers, but have little effect on wind- and ballistically-dispersed seeds.

Many studies in the tropics have shown that seed-dispersing birds and mammals avoid open grass areas and that a return to forest cover increases animal seed dispersal (Reviewed by Wunderle 1997). Although *L. leucocephala,* which dominates exotic forest stands in the dry forest zone of Puerto Rico (Ramjohn 2004), does not produce fruits that attract frugivorous animals, it does increase the structural complexity when it establishes in open grasslands and provide perches where dispersers may come to rest or nest. Furthermore, seeds that are dispersed

by animals to exotic forests may have an increased chance of germinating compared to seeds that fall from crowns. Mechanical scarification – a surrogate for animal-dispersal – has been shown to increase germination in many of the tree species native to the dry forest zone of Puerto Rico (Carvajal 2001). Further evidence that these exotic forests facilitate the dispersal and establishment of native trees was demonstrated by Pérez Martínez (2007). In nine secondary-forest stands with *L. leucocephala*-dominated canopies located throughout the dry forest zone of Puerto Rico he found that animal-dispersed tree species accounted for 83% (35 of 42) of the species of saplings encountered in the understory. Animal-dispersed species had the highest importance value in the sapling category at four of the nine sites. At three other sites an animal-dispersed species was second in importance only to *L. leucocephala. Croton humilis* was more important at the two other sites.

Understory vegetation type (grass vs. woody) had no clear effects on the patterns of seed rain for any seed type. While studies in Puerto Rico have shown that understory vegetation in pine and mahogany plantations can affect habitat use by frugivorous birds (Cruz 1987, 1988), the seed rain in this study was apparently unaffected by the dominance of grass in the understory. Another consideration is that grass tussocks may intercept falling seeds and trap them in their crowns, preventing them from reaching the soil and reducing their chances of successfully germinating and surviving. This question cannot be addressed with my results because the grass was continually cleared from the area directly above the traps, but it is a potential factor limiting tree regeneration in open grass areas and areas with high grass coverage in the understory.

Management implications

Exotic forests dominated by *L. leucocephala* develop on abandoned farmlands and burned areas in the dry forest zone of Puerto Rico due to factors subsequent to seed dispersal limitation. Although seeds of native tree species, especially those that are abiotically-dispersed, arrived to open grass areas at densities similar to seeds of *L. leucocephala*, native species rarely recruit to seedling and sapling stages in these areas (Francis and Parrotta 2006). These results combined with Ray and Brown's (1995), who showed that native dry forest tree species have low germination and survival rates in grassy areas of the Virgin Islands, suggest that direct seeding with native tree species is impractical for reforesting burned areas. Ray and Brown (1995) also showed that native species do not perform well when planted as seedlings in grassy areas and

suggested the use of *L. leucocephala* as a nurse tree for plantings of native seedlings. My results suggest that *L. leucocephala*-dominated areas may facilitate native tree recruitment without further management by attracting seed dispersers. Simply allowing *L. leucocephala* to grow in degraded areas and preventing further burning may eventually restore the tree species composition of undisturbed forest.

Table 3.1. Characteristics of the vegetation and land-use history at each of the seed trapping sites. Values are means and standard deviation for the five traps in each vegetation type at each site. Tree density and percent *L. Luecocephala* were calculated using the ten trees nearest each trap.

Site	**Vegetation type**	**Tree Density (m^{-2})**	**Percent *L. leuco-cephala***	**Percent grass cover**	**Land-use history**
	Native Forest/Woody	0.59 (0.25)	0 (0)	0 (0)	Selective cutting and goat grazing *c.*80 yr prior
	Native Forest/Grass	0.19 (0.06)	0 (0)	36 (24)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 25 yr prior
Cuevas	Exotic Forest/Woody	0.48 (0.31)	44 (11)	0 (0)	Cattle grazing and agriculture *c.* 80 yr prior
	Exotic Forest/Grass	0.37 (0.15)	86 (17)	30 (25)	Cattle grazing and agriculture *c.* 80 yr prior
	Open grass	0.06 (0.02)	2 (4)	58 (21)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 25 yr prior
	Native Forest/Woody	0.26 (0.06)	8 (4)	0 (0)	Selective cutting prior
	Native Forest/Grass	0.27 (0.10)	25 (17)	33 (15)	Selective cutting prior, grazing?
Ensenada	Exotic Forest/Woody	0.45 (0.38)	56 (22)	0 (1)	Cattle grazing, bulldozed *c.* 20 yr prior
	Exotic Forest/Grass	0.24 (0.13)	64 (18)	45 (21)	Cattle grazing, bulldozed *c.* 20 yr prior
	Open grass	0.06 (0.03)	42 (19)	83 (10)	Cattle grazing, bulldozed *c.* 20 yr prior, wildfire?
	Native Forest/Woody	0.37 (0.12)	8 (11)	0 (0)	Selective cutting and goat grazing *c.*80 yr prior
	Native Forest/Grass	0.11 (0.04)	40 (10)	23 (21)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 8 yr prior
La Hoya	Exotic Forest/Woody	0.43 (0.20)	70 (25)	0 (0)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 8 yr prior
	Exotic Forest/Grass	0.54 (0.27)	82 (16)	37 (18)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 8 yr prior
	Open grass	0.11 (0.04)	76 (11)	42 (25)	Selective cutting and goat grazing *c.* 80 yr prior, wildfire 8 yr prior
	Native Forest/Woody	0.68 (0.67)	7 (16)	0 (0)	Selective cutting and goat grazing *c.*80 yr prior
	Native Forest/Grass	0.19 (0.06)	0 (0)	28 (14)	Selective cutting and goat grazing *c.*80 yr prior, wildfire?
Pitirre	Exotic Forest/Woody	0.79 (0.72)	100 (0)	2 (2)	Agriculture *c.* 20 yr prior
	Exotic Forest/Grass	0.20 (0.05)	100 (0)	49 (20)	Agriculture *c.* 20 yr prior
	Open grass	0.04 (0.01)	72 (41)	61 (40)	Selective cutting and goat grazing *c.*80 yr prior, repeatedly burned

Table 3.2. Count of seeds collected throughout the study (July 2007 - June 2008). Counts for each species were summed among all traps (Total) and among the five traps within each vegetation type at each site. C = Cuevas, E = Ensenada, H = La Hoya, P = Pitirre

(a) Trees

Family	Species	Disp.	Total	Site	Vegetation type (Canopy/Understory) Exotic Canopy/ Grass	Exotic Canopy/ Woody	Native Canopy/ Grass	Native Canopy/ Woody	Open Grass
Leguminosae	*Leucaena leucocephala* (Lam.)de Wit ***	Auto	11582	C	460	749	0	0	0
				E	317	415	96	0	5
				H	589	140	49	6	373
				P	6180	1913	0	211	79
Nyctaginaceae	*Pisonia albida* (Heimerl) Britton, ex Standl.	Epi	7065	C	1	1	0	4	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	7059	0
Combretaceae	*Bucida buceras* L.	Auto	4508	C	0	0	9	314	0
				E	2	6	14	2156	0
				H	26	5	1070	352	70
				P	0	0	349	99	1
Rubiaceae	*Exostema caribaeum* (Jacq.) Roem & Schult.	Anem	1470	C	1	1	69	54	7
				E	0	1	0	27	0
				H	64	16	286	913	29
				P	0	0	2	0	0
Moraceae	*Ficus citrifolia* Mill.	Zoo	1027	C	0	0	0	565	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	432	0
Sapindaceae	*Thouinia portoricensis* Radlk.	Anem	599	C	0	1	64	28	31
				E	0	0	2	3	0
				H	20	3	19	357	2
				P	0	5	36	28	0
Rhamnaceae	*Colubrina elliptica* (Sw.) Briz. & Stern	Auto	562	C	1	0	0	168	1
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	318	74	0
Boraginaceae	*Bourreria succulenta* Jacq.	Zoo	458	C	0	0	0	17	0
				E	2	5	346	1	0
				H	0	24	37	24	0
				P	0	0	0	2	0
Leguminosae	*Prosopis pallida* (H. & B. ex Willd) HBK. ***	Zoo	264	C	0	0	0	0	0
				E	124	58	0	0	0
				P	0	82	0	0	0
				H	0	0	0	0	0

Table 3.2 continued

(a) Trees (continued)				Site	Vegetation type (Canopy/Understory)				
Family	**Species**	**Disp.**	**Total**		**Exotic Canopy/ Grass**	**Exotic Canopy/ Woody**	**Native Canopy/ Grass**	**Native Canopy/ Woody**	**Open Grass**
Rubiaceae	*Guettarda elliptica* Sw.	Zoo	252	CEHP	0 0 28 0	1 0 0 0	0 0 221 0	0 0 1 0	0 0 1 0
Burseraceae	*Bursera simaruba* (L.) Sarg.	Zoo	135	CEHP	0 1 0 0	1 0 0 2	38 2 0 6	9 4 5 67	0 0 0 0
Sterculiaceae	*Helicteres jamaicensis* Jacq.	Auto	134	CEHP	0 0 0 0	0 0 0 0	0 0 0 0	0 134 0 0	0 0 0 0
Rhamnaceae	*Krugiodendron ferreum* (Vahl) Urban	Zoo	96	CEHP	0 0 0 1	0 0 2 0	0 0 0 0	2 0 91 0	0 0 0 0
Cactaceae	*Cephalocereus royenii* (L.) Britton & Rose	Zoo	96	CEHP	0 0 0 0	6 0 0 0	0 0 0 24	0 0 0 66	0 0 0 0
Myrtaceae	*Eugenia rhombea (Berg) Krug & Urban*	Zoo	90	CEHP	0 0 90 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	Anem	61	CEHP	0 0 5 0	0 1 8 0	0 0 2 0	30 9 3 0	1 0 2 0
Leguminosae	*Pithecellobium unguis-cati* (L.) Benth.	Zoo	53	CEHP	0 0 0 0	0 2 0 0	0 0 0 0	0 51 0 0	0 0 0 0
Euphorbiaceae	*Euphorbia petiolaris* (Sims)	Auto	47	CEHP	0 0 0 0	3 0 0 0	0 0 0 0	0 0 0 44	0 0 0 0
Euphorbiaceae	*Savia sessiliflora* (Sw.) Willd.	Auto	43	CEHP	0 0 0 0	0 0 0 0	0 0 43 0	0 0 0 0	0 0 0 0

Table 3.2 continued

(a) Trees (continued)					Vegetation type (Canopy/Understory)				
Family	**Species**	**Disp.**	**Total**	**Site**	**Exotic Canopy/ Grass**	**Exotic Canopy/ Woody**	**Native Canopy/ Grass**	**Native Canopy/ Woody**	**Open Grass**
Euphorbiaceae	*Adelia ricinella* L.	Auto	35	C	0	0	0	0	0
				E	0	0	0	0	0
				H	0	0	0	0	35
				P	0	0	0	0	0
Capparaceae	*Capparis cynophallophora* L.	Zoo	31	C	0	0	0	0	0
				E	0	1	28	2	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Erythrox-ylaceae	*Erythroxylum areolatum* L.	Zoo	22	C	0	1	0	0	0
				E	4	6	1	1	0
				H	0	0	1	0	0
				P	6	0	0	2	0
Leguminosae	Cassia polyphylla Jacq.	Auto	16	C	16	0	0	0	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Myrtaceae	Eugenia foetida Pers.	Zoo	14	C	0	0	6	5	0
				E	0	0	0	1	0
				H	0	0	0	0	0
				P	0	0	0	2	0
Celastraceae	*Crossopetalum rhacoma* Crantz	Zoo	10	C	0	0	1	1	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	5	0	3	0
Rubiaceae	*Erithalis fruticosa* L.	Zoo	9	C	0	0	0	0	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	9	0
Erythrox-ylaceae	Erythroxylum sp.	Zoo	4	C	0	0	0	0	0
				E	0	3	0	0	0
				H	0	1	0	0	0
				P	0	0	0	0	0
Leguminosae	*Pictetia aculeata* (Vahl) Urban	Auto	4	C	0	0	0	4	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Euphorbiaceae	*Gymnanthes lucida* Sw.	Auto	2	C	0	0	0	2	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Capparaceae	*Capparis sp.*	Zoo	1	C	0	0	0	1	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0

Table 3.2 continued

(b) Vines and Epiphytes				Site	Vegetation type (Canopy/Understory)				
Family	**Species**	**Disp.**	**Total**		**Exotic Canopy/ Grass**	**Exotic Canopy/ Woody**	**Native Canopy/ Grass**	**Native Canopy/ Woody**	**Open Grass**
Vines									
Rhamnaceae	*Gouania lupuloides* (L.) Urb.	Anem	4391	C	272	844	0	0	0
				E	1796	959	6	0	6
				H	44	132	304	23	5
				P	0	0	0	0	0
Bignoniaceae	*Macfadyena unguis-cati* (L.) A. H. Gentry	Anem	379	C	0	127	0	2	0
				E	2	104	3	38	0
				H	65	22	8	2	6
				P	0	0	0	0	0
Sapindaceae	*Serjania polyphylla* (L.) Radlk.	Anem	225	C	2	0	0	0	0
				E	72	121	14	8	0
				H	4	2	0	0	2
				P	0	0	0	0	0
Connaraceae	*Convolvulus nodiflorus* Desr.	Auto	196	C	0	0	1	2	0
				E	0	0	12	0	0
				H	0	0	172	0	1
				P	0	0	0	0	0
Oleaceae	*Jasminum fluminense* Vell.***	Zoo	193	C	1	0	0	2	0
				E	26	2	4	2	0
				H	28	84	6	14	0
				P	4	19	1	0	0
Leguminosae (Faboideae)	*Teramnus labialis* (L. f.) Spreng.	Auto	111	C	1	0	2	17	0
				E	7	0	11	0	0
				H	6	0	3	0	0
				P	0	0	0	64	0
Bignoniaceae	*Distictis lactflora* (Vahl) DC.	Anem	5	C	0	1	0	0	0
				E	0	1	0	0	0
				H	0	0	2	1	0
				P	0	0	0	0	0
Asclepiad-aceae	*Matelea maritima* (Jacq.) Woodson	Anem	2	C	0	0	0	0	0
				E	0	0	0	0	0
				H	0	0	2	0	0
				P	0	0	0	0	0
Epiphytes									
Bromeliaceae	*Tillandsia sp.*	Anem	144	C	0	99	0	0	0
				E	0	0	0	45	0
				H	0	0	0	0	0
				P	0	0	0	0	0

Table 3.2 continued

(c) Shrubs/forbs and Unknown Form				Site	Vegetation type (Canopy/Understory)				
Family	**Species**	**Disp.**	**Total**		**Exotic Canopy/ Grass**	**Exotic Canopy/ Woody**	**Native Canopy/ Grass**	**Native Canopy/ Woody**	**Open Grass**
Shrubs/Forbs									
Euphorbiaceae	*Croton sp.*	Auto	228	C	0	0	115	25	9
				E	0	0	0	0	7
				H	0	0	0	0	0
				P	0	0	67	5	0
Verbenaceae	*Lantana sp.****	Zoo	222	C	0	0	0	0	0
				E	92	0	2	0	0
				H	96	24	0	0	7
				P	0	0	0	1	0
Leguminosae	*Desmodium glabrum* (Mill.) DC.	Epi	47	C	0	0	37	0	3
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	1	2	4
Malvaceae	*Gossypium barbadense* L.	Anem	38	C	0	0	0	0	0
				E	38	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Leguminosae	*Coursetia caribaea* (Jacq.) Lavin	Auto	9	C	0	8	0	0	1
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	0	0	0
Unknown Form									
Leguminosae	*Unk sp.*	Unk	32	C	0	0	6	0	19
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	5	2	0
Euphorbiaceae	*Unk sp.*	Zoo	7	C	2	0	0	0	0
				E	0	0	0	0	0
				H	0	0	0	0	0
				P	0	0	1	3	1
Bignoniaceae	*Unk sp.*	Anem	3	C	0	0	0	0	0
				E	0	0	0	0	0
				H	0	0	0	3	0
				P	0	0	0	0	0
Unknown	*Unk sp.*	Var	688	C	22	18	44	45	21
				E	47	65	70	41	1
				H	10	19	45	87	42
				P	5	6	37	49	14

Dispersal syndrome abbreviations
Anem – Anemochory (Wind)
Auto – Autoboleochory (Ballistic)
Epi – Epichory (Clinging)
Unk - Undetermined
Var - Various
Zoo - Zoochory (Animal)
*** Indicates exotic species

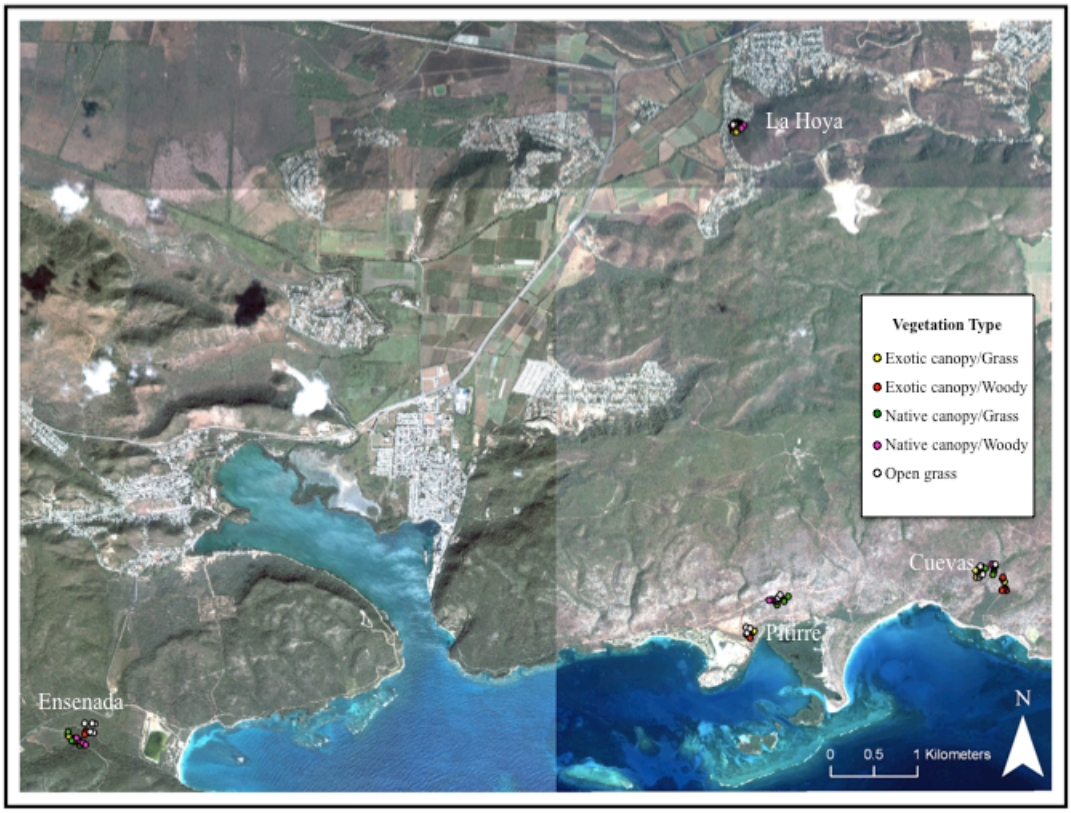

Figure 3.1. Satellite image of Guánica Forest and surrounding area. Seed trap locations were taken with a GPS unit and are marked with colored circles.

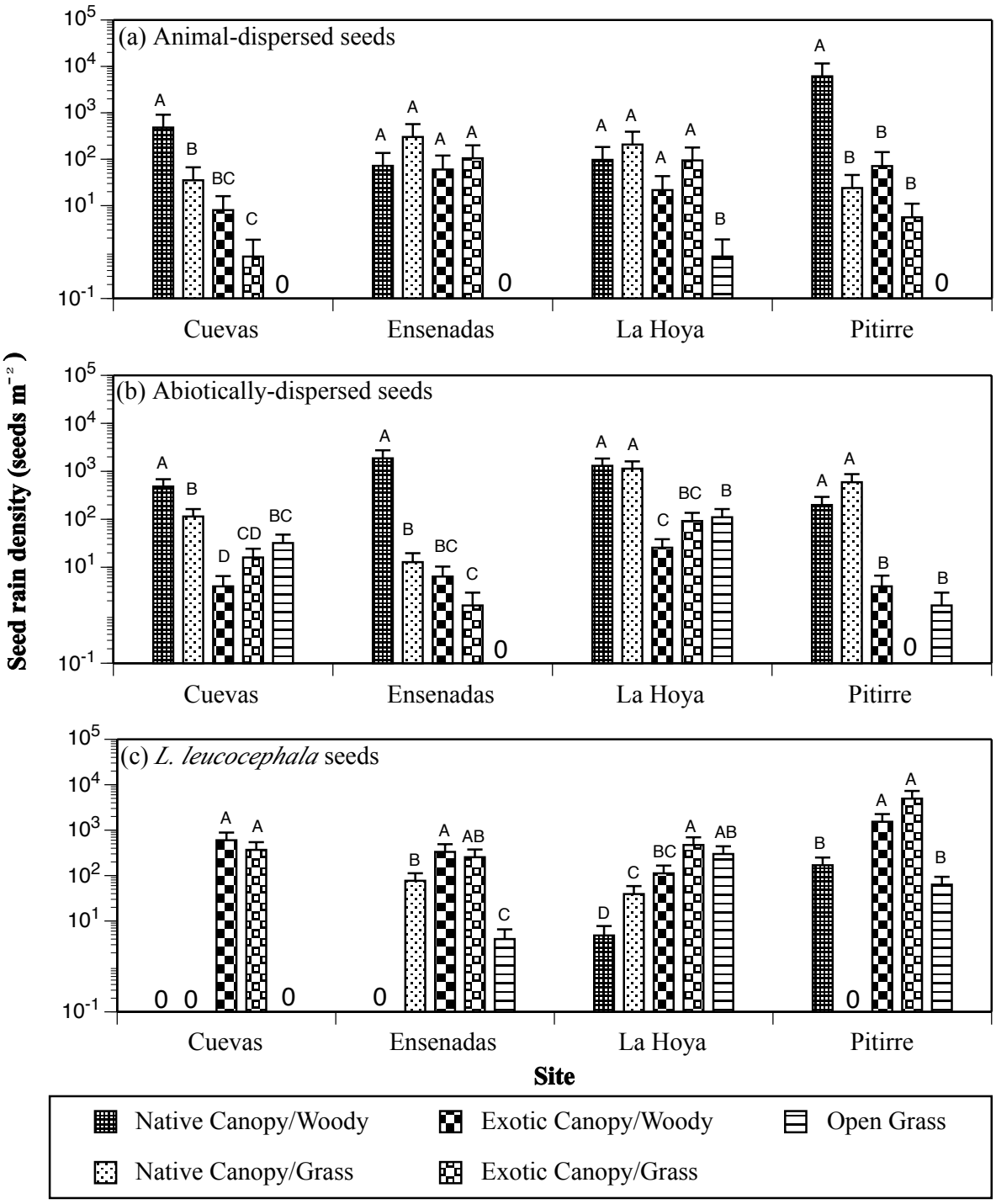

Figure 3.2. Mean one-year (July 2007–June 2008) tree seed rain densities in four sites and five vegetation types within Guánica forest. Seeds are categorized among (a) animal dispersed, including zoochoric and epichoric seeds; (b) abiotically-dispersed, including anemochoric and autoboleochoric seeds; and (c) *L. leucocephala* seeds, which are autoboleochoric. The vertical axis is log scaled. Bars are SE. Within site and seed type, bars that that share letters are not significantly different with Fisher LSD ($\alpha = 0.05$).

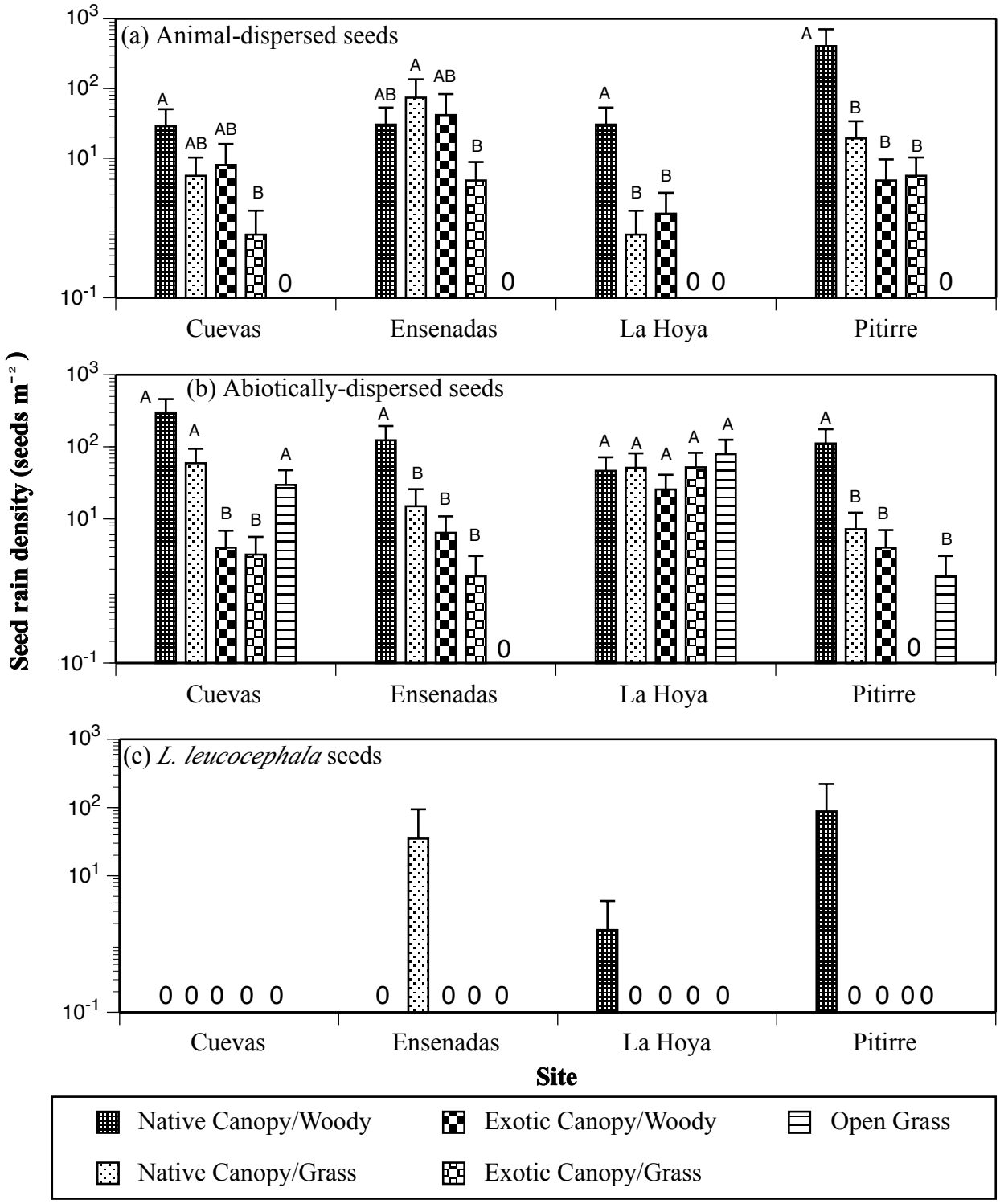

Figure 3.3. Mean one-year (July 2007–June 2008) tree seed rain densities after subtracting from the count the species with trees within the ten nearest trees to each trap. Data are presented in the same format as figure 2.

Chapter 4

Performance of *Leucaena leucocephala* and native saplings planted in grass-dominated areas subjected to burning within Guánica Forest, Puerto Rico

Introduction

Dry forests covered large areas of the tropics before being cleared for agriculture and urban areas from pre-Columbian to present times (Murphy and Lugo 1986a). Today these land uses form a matrix that encompasses the remaining patches of tropical and subtropical dry forest (TDF) (Miles et al. 2006). Exotic grasses, often introduced as forage crops, limit forest regeneration in degraded TDF by promoting a high-frequency fire regime that inhibits tree recruitment. These fires often extend into adjacent intact forests, further threatening TDF (Janzen 1988, D'Antonio and Vitousek 1992, Mueller-Dombois 2001).

In the absence of fire, trees may eventually recolonize burned areas and form a closed canopy that shades out grasses in the understory (Janzen 1988, Higgins et al. 2000). However in the subtropical dry forests of Puerto Rico, cleared dry forest areas that are left unburned become dominated by the naturalized legume tree *Leucaena leucocephala* (Lam.) de Wit (subfamily Mimosoideae) for at least 60 years after fire, while native trees slowly increase in importance with time (Weaver and Chinea 2003, Francis and Parrotta 2006, Molina Colón and Lugo 2006, Pérez Martínez 2007, Weaver and Schwagerl 2008).

This pattern of naturalized- or exotic-tree dominance may be explained by microhabitat shifts in exotic grass communities that range outside the tolerance of native trees. Increased solar irradiance in open areas has been shown to increase seedling mortality of native species in other Caribbean TDFs (Ray and Brown 1995, McLaren and McDonald 2003b). High light levels have been shown to cause photoinhibition in saplings planted in abandoned pastures in Costa Rica (Loik and Holl 2001) and overheating due to reduced transpirative cooling when stomata are closed to reduce water loss (Callaway 1995). Exotic species, such as *L. leucocephala* may dominate secondary forests because they are better able to grow under these conditions.

I predicted that the long-term demographic trends in burned areas of Puerto Rican TDF could be explained by the initial performance of saplings in exotic grass-dominated areas.

Planted saplings were used to test the following hypotheses: (1) saplings of native species have lower growth and survival rates in grass dominated areas than in the forest understory, (2) *L. leucocephala* has higher growth and survival in grass dominated areas than under forest canopies, (3) *L. leucocephala* survives and grows more than native species when subjected to wildfire. An additional objective of this study was to identify native species effective for reforesting grass-dominated areas or resistant to grass-fueled wildfire.

Methods

Study site

Saplings were planted in and near three areas along the coastal road Rt. 333 that had periodically burned in prescribed or arson fires for more than 10 years prior to this study. The sites ranged 5 to 20 m above sea level (ASL) and 5 to 500 m inland from the coast. Site 1 was situated 5 m ASL, 20 m inland, and separated from the sea by a strip of mangrove trees and Rt. 333. Site 2 was situated 20 m ASL, 500 m inland and separated from the sea by mangrove forest, a small housing community, and scrub forest. Site 3 was situated 5 m ASL and set back 5 m on a seaside cliff top. The burned areas were dominated by *Pennisetum ciliare* (L.) Link (buffel grass) and to a lesser extent *Bothriochloa pertusa* (L.) A. Camus. (hurricane grass). Site 3 also had small patches of *Urochloa maxima* (Jacq.) R.D. Webster (guinea grass). Nearby forest stands were dominated by *Bucida bucerus* and *Bursura simaruba* trees and had little or no grass in the understory. These two deciduous tree species account for the majority of the basal area in the scrub forest area of Guánica Forest (Lugo et al. 1978).

Sapling species and rearing

Saplings of 14 tree species were used in this study, representing a variety of morphological characteristics and the general availability from public and private nurseries in Puerto Rico of saplings suitable to the dry forest zone (Table 4.1). Saplings were acquired from a variety of sources from May through September 2007, and cultivated in the U.S. Fish and Wildlife Service Cabo Rojo National Wildlife Refuge nursery prior to transplanting them at the study site in October 2007. Individuals from each species were randomly selected for treatments and acclimated by placing them in full sun or the shade of large trees for 4 weeks prior to transplanting. All saplings were hardened by gradually decreasing the watering interval until

they received water only once a week before planting. At the time of planting, each sapling was placed with the soil from its pot and 50 mL of granular super-phosphate fertilizer (0-50-0) into a pre-dug hole and watered with 8 L of water. Mean height at the time of planting ranged from 42 to 169 cm among species (Table 4.1). The saplings were watered with 8 L of water eight times before the start of the early-summer rainy season in April 2008 to encourage establishment. Watering was applied when 7 consecutive days passed without at least 10 mm of rainfall. Thereafter, watering was stopped so that performance of the plants could be assessed in the drought conditions that are common in Guánica Forest (Lugo et al. 1978).

Planting design and prescribed fires

At each site saplings were placed in three treatments: forest understory, open grass, and open grass subjected to a controlled burn. Saplings were planted in plots with one individual of each species arranged randomly and spaced *ca*. 1 m x 1 m. Eight plots were planted in the grass and three plots in the forest at each site. Some species were short of replicates and in five cases other species were mistakenly planted twice within a plot, so the total number of individuals of each species ranged from 25 to 35 and the total was 455 saplings (Table 4.1).

Prescribed fires were applied to the planting sites, along with other grassy areas along Rt. 333, on February 22, 2008. This date was chosen because it was near the time that grasses became fully cured, allowing them to burn completely and prevent future, uncontrolled fires. Back burns were applied around the periphery at each site, followed by head-fires. Characteristics of the fires are described in Table 4.2. Three to four planting plots at each grass site were randomly selected to be burned beforehand. The remaining plots were protected from the fires by trimming the grass to ground level and raking away the litter within 2 m of the saplings before the fires were applied. During the prescribed burn at Site 3, the fire breaks failed to stop the fire from entering three of the fire-protected plots and a section of the fourth plot. These plots and the burned section of the fourth were subsequently treated as a separate treatment for analysis of fire characteristics – cut-grass burned. The grass around all surviving saplings was cut and raked again at the beginning of the dry season in December 2008 to prevent further burning.

Measurements of sapling performance

The saplings were measured for growth at the time of planting and 4, 8, and 12 months afterwards. Height was measured as the distance above the ground of the highest live meristem, straightening stems if they were bent. Basal diameter was measured at 5 cm above ground level. This height was marked with a permanent marker to improve the precision of remeasurements. Basal diameter was calculated as the average of two perpendicular measurements taken with calipers to the nearest 0.1 mm. To compare treatment effects on basal sprouting all stems branching from the main stem below 30 cm height were measured for their height above the ground and their length. Plant survival was monitored monthly by checking for the presence of living leaves or green stems.

Measurements of fire characteristics

Measurements of fuel loads and peak fire temperatures were made at Sites 1 and 3 only. These measurements were precluded at Site 2 by an arson fire that burned two days prior to the scheduled prescribed burns. Pre-burn fuel loads and the amount of combusted fuel were estimated in six randomly placed 0.5 m x 0.5 m plots at each site. The day before the prescribed fires were applied, all plant material was collected in a rectangular half of each plot and the space extending upward from this area. Two days after the prescribed fires, the remaining plant material was collected in the other half of each plot. The collections were oven dried at 65°C for four days, separated between fine and coarse (>5 mm diameter) material, and weighed. The amount of biomass that burned in each plot was calculated as the difference between the masses of pre- and post-fire collections. Only fine material was used in the analysis because calculations using coarse materials are unreliable with this technique due to their spatial heterogeneity (J. Thaxton, personal communication).

Peak fire temperatures were measured around the planted saplings with temperature-sensitive paints and chalks (Omega Engineering Inc., Stamford CT). Heavy-duty aluminum foil 10 x 2 cm strips were marked with paints rated to melt at 79, 93, 107, 121, 135, 149, 163, 177, 204, 260, 316, 427 and 538°C. Fine-grain (320 grit) waterproof sandpaper cut into 5 x 1 cm strips were marked with chalks rated to melt at 52, 66, 79, 93, 107, 121, 135, 149, 163, and 177°C. The two strips were enclosed in another layer of foil to avoid ash from obscuring the results. Immediately before the prescribed fires, the strips were staked to the ground at the base

of each sapling and wrapped loosely around their stems at 50 cm and 100 cm height on saplings that reached these heights. Peak temperatures were measured as the highest temperature paint or chalk that melted. Where the paints and chalks had overlapping temperature ranges, they showed high agreement in measurements (14 ± 3°C mean difference). Readings from the paint strip were used for temperatures >79°C and readings from the chalk strip were used for temperatures of 52 and 66°C. This may slightly underestimate the peak temperature within the intervals between paints (see Kennard et al. 2005).

Measurements of environmental parameters

Weather measurements from the Western Regional Climate Center (WRCC, www.wrcc.dri.edu) were used for comparison of temperature, relative humidity, and wind speed during the prescribed fires and daily precipitation throughout the study. The weather monitoring station was located in Guánica Forest near Route 333, within 2 km of the planting sites.

Leaf area index (LAI, a unitless measure of canopy cover defined as the ratio of leaf surface area to ground surface area) measurements were made with an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE). Measurements were taken in the dry season, when LAI is generally lowest due to deciduous leaf fall, and again in the wet season, when LAI is generally highest (Murphy and Lugo 1986b). LAI was measured at the plot level by interpolating measurements taken at 9 randomly selected points within each plot with reference measurements taken before and after in a clearing (> 30 m from the nearest tree). The machine then calculated LAI ± SE for each plot by comparing the reference and plot measurements, assuming a maximum transmittance of 1.0 in the plots. Measurements were taken on a uniformly overcast day in the dry season (April 3, 2008) and during sunset (1630 – 1730 h) for two days in the wet season (October 30 and November 3, 2008).

Data Analysis

Pre-fire fuel loads and percent of fuel consumed were compared between Sites 1 and 3 with Student's *t*-tests. Peak fire temperatures were compared among Site 1, Site 3 plots with cut grass, and Site 3 plots with uncut grass using ANOVA. Each of these was treated as a separate treatment and plots within each treatment were treated as random nested factors. Nested within the plots were the individual trees with temperature strips at one to three heights. Height was

treated as a subplot factor within a tree. Tukey-Kramer comparisons were used to separate significant differences ($p < 0.05$). The value 38°C was used in the calculations when temperature strips did not register the minimum 52°C (n = 0 at ground level, n = 5 at 50 cm height, n = 4 at 100 cm height). This temperature was the midpoint between 52°C and the mean air temperature during the prescribed fires (25°C).

A split-plot ANOVA was performed to test for differences in LAI among sites, treatments (grass and forest), and season (dry and wet). Values were transformed [Log (LAI + 1)] prior to the analysis to meet the assumptions of normality and homogeneous errors.

Logistic regression was used to identify factors that influenced sapling survival in the burned treatment. Saplings that resprouted at any time after the burn were classified as survivors. Predictors of survival in the logit model were fire temperatures at ground level and 50 cm height (100 cm height was not used because of low sample size), stem diameter, height, and total shoot length. Additionally, chi-square tests were used to test for differences in survival among species and planting sites (with Site 3 divided between cut and uncut grass).

Survival rates across the first 15 months after planting were compared among treatments and species using a Cox proportional hazard ratio model. This test uses a semi-parametric regression model without underlying assumptions of error distribution that is well suited for datasets with mortality that are effected by seasonality and sample units that are censored because they either survived to the end the study or were removed before mortality occurred (Fox 1993). A model with treatment, species, and their interaction as independent variables was tested first. The interaction term was not significant ($p > 0.1$) and was therefore removed from the model to improve the power of the test. The forest treatment and *L. leucocephala* were used as baseline values with which the hazard ratios for each effect were computed. Values >1 indicate an increased risk of mortality and <1 a decreased risk compared to the baselines.

Differences among species and treatments in growth were tested using blocked (site) two-way (species and treatment) random nested (plot within site) ANOVAs with change in basal diameter and height as the dependent variables. These values were calculated as the difference between initial and one-year measurements. Saplings that did not survive the first year after planting were not included in the growth analyses. The burned grass treatment was excluded from these tests because of low replication; instead, in the burned grass treatment (cut and uncut grass combined), growth was assessed as live stem height and total auxiliary shoot length (sum

of lengths of all shoots branching from the main stem) of the nine burned plants that survived to one year. Because three of the native species had only a single surviving plant, native species were pooled and compared to *L. leucocephala* with Student's t-tests.

Results

Fire Characteristics

The average amount of pre-fire fine fuel was not significantly different between sites 1 and uncut areas of site 3 (616 ± 72 and 476 ± 95 $g \cdot m^{-2}$ respectively; $t = 1.2$, df = 10, p >.2; Table 2). Nor did the amount of fuel consumed in the fires differ (90 ± 4 and 90 ± 2% respectively; $t = 0.16$, df = 10, p > .5; Table 2). Although fuel loads were not measured at Site 2, they were visibly similar to the measured plots. In the cut-grass plots at Site 3, fuel loads were much lower, but they still proved sufficient to carry the flames across their entire area. Burn treatment (Site 1, Site 3 cut-grass, Site 3 uncut-grass) and height (0, 50, 100 cm height) were both significant factors affecting mean peak fire temperatures, while the interaction between these factors was not significant (p=0.06; Appendix C). Temperatures were highest at ground level at all three sites and varied significantly only between the uncut and cut plots at site 3 (Table 4.2, Figure 4.1). At 50-cm height, peak temperatures were significantly lower in the Site 3 cut-grass plots than both the Site 1 plot and Site 3 uncut plots while at 100 cm no difference in peak temperature was detected among the three treatments (Table 4.2)

Peak temperatures that the planted saplings experienced were likely reduced by the grass removal and topsoil disruption caused while planting. Twelve additional peak temperature measurements were made in the biomass plots at Sites 1 and 3. Three of these reached 427°C and nine reached the measurable maximum of 538°C. Three of the strips had melted aluminum, which occurs at 660°C. These results indicate that grassy areas undisturbed by planting had a mean peak temperature at ground level of *ca.* 540°C. None of the aluminum strips that were placed on the planted saplings had melted sections after the fires. This indicates that while the peak temperatures measured as 538°C may have been underestimated, they were never underestimated by >122°C, which is similar to the next highest interval that was used (i.e., 111°C between 427 and 538°C).

Environmental parameters

LAI varied significantly with treatment, season, and the treatment x season interaction, but not among the planting sites (Figure 4.2, Appendix C). LAI was near zero in the grass treatments because shade above the grass canopy came only at angles near the horizon from trees in the vicinity of the plots. LAI was an order of magnitude greater in the forest plots than the grass plots. The interaction term was significant because LAI increased during the wet season by 1.5 in the forest plots and only 0.06 in the grass plots (Figure 4.2).

Plant survival

All of the saplings in the burn treatment had their entire canopy scorched in the prescribed fires. Their leaves were charred in the fire or turned brown within a few days of burning, presumably due to overheating. Excepted from this was one *P. aculeata* at Site 1 that registered a peak temperature of < 52°C and showed no effects after the fire. The grass bordering this plant did not burn either so it was classified in the unburned grass treatment for analysis. Those plants that survived the fires resprouted from the roots, root collar, and/or stems up to 175 cm height. A total of 67 of 184 (36.4%) saplings that burned resprouted, most within 5 months of the fire. The proportion of saplings that survived the fire (as evidenced by resprouting) varied significantly among the three planting sites [Site 2 (85%) > Site 1 (30%) ≈ Site 3 cut-grass (24%) > Site 3 uncut-grass (0%); $\chi^2 = 85.5$, df = 3, $p < 0.001$], but not among species (range 16.6 – 66.6%; $\chi^2=10.0$, df=13, $p > 0.1$). The logit regression model showed that peak fire temperature at ground level was a significant predictor of plant survival ($\chi^2 = 11.5279$, df = 1, $p < 0.001$; Figure 4.3) while temperature at 50 cm height and plant height, basal diameter, and total shoot length were not ($p > 0.05$). For each 50°C increase in peak temperature at ground height the odds of plant survival decreased by a factor of 0.655.

Survival rates at the end of 15 months were 4.6, 47.1, and 61.8% in the burn, grass, and forest treatments respectively (Figure 4.4). The saplings experienced high mortality in all three treatments during the summer 2008 dry season. Starting June 15, 60 days passed with only 32.8 mm of rain and two days with >10 mm of rain. Between the July and August measurements, plant survival dropped by 74.3, 42.5, and 19.2% in the burn, grass, and forest treatments respectively. Survival rates stabilized again at the onset of the fall 2008 wet season and into the winter 2009 dry season despite similar drought conditions in December 2008 – January 2009

(Figure 4.4). The Cox proportional hazard ratio analysis showed that both the burn and grass treatments had significantly greater risk of mortality than the forest treatment (burn: b = 5.94, χ^2 = 105.95, df=1, p < 0.0001; grass: b = 1.45, χ^2 = 3.91, df = 1, p = 0.048). Mortality risk was also higher in the burn treatment compared to the grass treatment (b = 4.08, χ^2 = 91.35, p < 0.0001). After 15 months, species survival rates in the three treatments combined ranged from 12.1% (*T. heterophylla*) to 60.6% (*L. leucocephala*) (Figure 4.5). When compared to *L. leucocephala,* the native species had hazard ratios ranging 1.22 to 3.31 that were significantly >1 for eight species (Figure 4.6). While the general trend was for lower survival in the grass than forest treatment, within species this was not always the case. Three species had equal or slightly higher survival in the grass than the forest (*B. succulenta, B. buceras, C. rhacoma*). This indicates that species may vary in their relative tolerance to the two treatments (Figure 4.5).

Sapling Growth

Overall, the saplings that survived the first year after planting had little change in basal diameter. The ANOVA model for basal diameter growth showed species, treatment, and the species x treatment interaction as significant factors while site was not (Appendix C). In the forest plots, mean diameter growth ranged from -1.3 to 2.0 mm among species and the only significant difference among species was that *C. diversifolia* and *P. subcordata* grew more than *T. heterophylla* (Figure 4.7a). In the unburned grass plots, species showed a larger range in mean diameter growth, from -1.2 to 11.7 mm. In this treatment *L. leucocephala* grew far more than the native species. Its mean growth was 11.7 mm while the next highest species, *C. uvifera,* grew 4.4 mm. Most species had higher mean diameter growth in the unburned grass plots than the forest plots; however, *C. uvifera* and *L. leucocephala* were the only species that differed significantly between the two treatments.

Growth in height was highly variable within species and treatments. Stem dieback was common and resulted in negative mean growth rates for nearly all species in the forest and grass plots. The ANOVA model showed site, species, and the species x treatment interaction as significant factors (Appendix C). No significant differences were found among species in the forest plots, while in the grass plots *B. simaruba* and *L. leucocephala* grew more than *C. fruticosum* and six species grew more (or shrunk less) than the single survivor of *T. heterophylla* (Figure 4.7b). Within species, no differences were found between the grass and forest plots.

In the burn treatment growth was assessed only on saplings that survived to November, 2008, eight months after the prescribed fires. These included three *L. leucocephala,* three *G. elliptica,* and one each of *B. simaruba, C. rhacoma,* and *C. fruticosum.* In t-tests that compared *L. leucocephala* to the native saplings pooled, *L. leucocephala* had a higher mean stem height (69 ± 23 cm versus 28 ± 13 cm; $t = 3.55$, df = 7, $p < 0.01$) and total shoot length (266 ± 83 cm versus 58 ± 37 cm; $t = 5.41$, df = 7, $p < 0.001$) than the native species 10 months after the fires; although they did not differ in the number of shoots per plant (10 ± 3 versus 5 ± 4 shoots per plant; $t = 1.92$, df = 7, $p > 0.05$) (Figure 4.8).

Discussion

Fire characteristics

Various factors combine to determine a fire's intensity, the most important being fuel load, topography, and climatic factors such as temperature, humidity, and wind (Whelan 1995). Peak fire temperature is an imperfect measure of fire intensity because it does not incorporate flame residence time, yet it is still a useful proxy with which to relate biotic responses (Bond and van Wilgen 1996, Kennard et al. 2005). Fine fuel loads and peak temperatures in this study correlated well with those of mixed-species grassland fires in Texas (Stinson and Wright 1968). Measurements of peak temperatures were highest at ground level in this study, although higher peak temperatures may have been found at a height between ground level and 50 cm height. Maximum peak temperatures vary vertically depending on structural attributes of the fuels and wind conditions (Whelan 1995). The low correlation between peak temperatures at ground level and 50-cm height (Figure 4.1) is likely a result of vertical variance in fuel loads combined with shifting winds during the fires.

Sapling response to burning and drought

Saplings were not tolerant to fire. They were more likely to survive burning when they experienced lower peak fire temperature near their base (Figure 4.3), but few burned saplings survived to the next wet season (Figure 4.4). While 36.4% of the saplings survived and resprouted after burning, only 4.6% survived the first year after planting. The water amendments that were applied until the onset of the summer wet season likely facilitated resprouting for saplings that survived burning, whereas exposing the saplings to the water deficits that typically

occur after the fires would have reduced their ability to resprout and exhibit their survival status. Watering allowed us to distinguish between death caused directly by burning and death caused by subsequent factors. The late summer drought reduced survival of burned saplings more quickly and to a greater degree than unburned saplings in the grass and forest plots (Figure 4.4). This may be because the burned saplings allocated their carbon reserves to shoot production and subsequently lacked maintenance reserves sufficient to survive through the extended period of water deficit. When the hazard ratio analysis was used to look at the effects of burning and drought together in the first 15 months since planting, risk of mortality was four and six times higher for burned saplings than for those planted in the unburned grass and forest respectively.

Immediate post-fire survival rates did not vary statistically among species, yet their rates ranged 16.6 to 66.6%, indicating that a lack of statistical power caused by low replication (Table 4.1) could be the reason rather than similar intrinsic fire survival among the species. When a wildfire entered a planting trial near Sierra Bermeja, Puerto Rico, ~20 km west of Guánica Forest, sapling survival rates were slightly higher than in this study. There, Santiago-García et al. (2008) found that 68% of 68 saplings of 23 native species planted in a *Urochloa maxima* grassland survived burning by resprouting despite having their entire stems charred. Survival rates were also higher when a wildfire entered a planting trial in northern Thailand. There, 63.5% of 570 saplings of 34 native species that burned in a "moderate litter fire" survived (Elliott et al. 2003). Survival among species ranged 22 to 100% and varied significantly among species (simple Chi square test performed on data in their Table 5: $\chi^2 = 109.7$, df = 34, $p < 0.001$). In Panama, seedlings planted as seeds in *Saccharum spontaneum* grassland ~8 mo before a wildfire burned the area had 6.7% survival whereas unburned areas had 57.2% (Hooper et al. 2005). The differences in survival rates among studies could be attributed to many factors, including the time since planting when the fires occurred, the size and condition of the saplings when they burned, and the intensity of the fires.

The saplings planted in the unburned grass experienced higher mortality than those planted in the forest plots during the seasonal drought in late summer 2008. These results agree with those of Ray and Brown (1995) who found that 3-6 mo-old seedlings of ten native tree species planted in an abandoned pasture in a U.S. Virgin Islands TDF had 9-mo survival rates of 0-65% (mean = 28.8%) while seedlings planted under 25%-PAR mesh cloth had survival rates of 45-90% (mean = 71.0%). Similarly, McLaren and McDonald (2003b) found that seedlings of

four native tree species germinated from seeds sown factorially in three light levels with and without watering in a Jamaican TDF had the highest mortality during a seasonal drought at higher light levels without watering. My study shows that the increased mortality of seedlings at high light levels continues in larger saplings planted in the field after > 1 yr of nursery growth.

Sapling growth

Growth in basal diameter was minimal and stem height was reduced by dieback in most saplings that survived the first year after planting (Figure 4.7). Severe desiccation and resultant xylem cavitation was probably the main cause of stem dieback, although some plants were also attacked by stem boring insects. Water stress likely limited growth during most of the study period, until the wet season began at the end of August 2008. The trend for increased basal diameter in the grass treatment, although only significant for one of the native species, could be due to higher light availability during the wet season. When water was available to saplings in the forests plots, LAI was at its peak and probably prevented the saplings from fully utilizing the available water. Although the forest canopy may have protected the saplings from drought stress in the dry season, it may have limited their growth during the wet season. The precipitation seasonality experienced by the saplings was not unusual in Guánica Forest. In June 2008, when 60 days passed with only 32.8 mm of rain the majority of the mortality occurred (Figure 4.4). The WRCC weather station began continuously recording rainfall near the planting sites in June 2005. From that time until May 20, 2009, four other periods have passed with >60 consecutive days with <33 mm of rain. The high seedling and sapling mortality caused by these droughts combined with slow growth and stem dieback is likely a major limitation to native forest regeneration in grass-dominated areas that do not burn.

In contrast to the native species, *L. leucocephala,* grew profusely in the grass treatment. This species was clearly better able than the native species to use the limited water and abundant light available in the grass plots. While the physiological traits that led this species to outperform the native species in the grass treatment were not identified in this study, they are likely adaptations associated with its functional niche in its indigenous range. In the Yucatán peninsula, Mexico, *L. leucocephala* is a pioneer that dominates areas after they incur wildfires sparked by lightning, often following hurricanes (Allen et al. 1993). These wildfires are often of high intensity and completely combust the thin organic soils overlaying karstic substrate (Vargas et al.

2008). *L. leucocephala* appears to have assumed the same role in Puerto Rican TDF since its introduction sometime before 1825 (Parrotta 1992). Because fires were infrequent or absent in Puerto Rican TDF prior to human disturbance (Murphy et al. 1995), this successional pathway was not prevalent. Disturbances common in Puerto Rico, such as hurricanes, do not create large clearings and regeneration is dominated by resprouting (Ewel 1977, Murphy et al. 1995, Van Bloem et al. 2005). Adaptation to this type of disturbance rather than fires may explain why native species perform poorly in areas of high light such as exotic grasslands.

Management implications

The high mortality of burned saplings indicates that fire is strong barrier to forest regeneration in grass dominated areas of Guánica Forest. Fires that inadvertently enter planting sites can cause costly setbacks to restoration efforts (Janzen 1988, Francis and Parrotta 2006). The risk of such fires is diminished when tree canopies close and the shade suppresses grass in the understory and consequently fuel loads. The native tree species planted in this study showed growth rates that would be unlikely to form a closed canopy in a practical timeframe; they would be exposed to the threat of fire for extended periods. However, *L. leucocephala* grew at an exceptional rate in the grass treatment and recovered the most of among all species in the burn treatment. Although, this species is considered highly invasive (Rejmanek and Richardson 1996), it does not appear to displace native TDF in Puerto Rico (Molina Colón and Lugo 2006). Apparently, its growth is greatly suppressed in forest understories (Figure 4.7). These results support the conclusions of other authors that have recommended using *L. leucocephala* for reforesting degraded sites in Puerto Rican TDF (Murphy 1916, Francis and Parrotta 2006, Santiago-García et al. 2008). Throughout much of its exotic range, *L. leucocephala* has been severely affected by a psyllid pest that defoliates young shoots (Gieger and Gutierrez 2000); although, in Puerto Rico this pest appears innocuous, as evidenced by the continued dominance of *L. leucocephala* in disturbed areas (Molina Colón and Lugo 2006). Using *L. leucocephala* as a nurse tree will increase natural forest regeneration and the success of underplanted native trees (Parrotta 1995, Ray and Brown 1995).

Table 4.1. The source; number; and initial measurements of height, basal diameter, and number of auxiliary shoots for the 14 tree species planted in this study. Numbers in parentheses are standard deviations.

						Initial Measurements		
Family	**Species**	**Source**	**N Forest**	**N Grass**	**N Burned**	**Height (cm)**	**Basal Diam. (mm)**	**N aux. shoots**
Boraginaceae	*Bourreria succulenta* Jacq.	FC	9	10	14	96 (16)	12 (1)	2.9 (2.9)
Combretaceae	*Bucida buceras* L.	FC	9	9	15	70 (26)	12 (2)	3.5 (2.7)
Burseraceae	*Bursera simaruba* (L.) Sarg.	RNG, FC	10	11	13	87 (22)	8 (2)	0.2 (0.7)
Verbenaceae	*Citharexylum fruticosum* L.	FWS	9	10	14	92 (30)	10 (2)	3.8 (2.6)
Polygonaceae	*Coccoloba diversifolia* Jacq.	FWS, FC	9	10	15	99 (35)	12 (4)	2.4 (1.5)
Polygonaceae	*Coccoloba uvifera* (L.) L.	Jardines Eniedas	9	12	12	83 (27)	15 (2)	1.0 (1.3)
Celastraceae	*Crossopetalum rhacoma* Crantz	Jardines Eniedas	9	11	14	98 (20)	11 (2)	3.9 (3.2)
Erythroxylaceae	*Erythroxylum areolatum* L.	RNG	9	9	17	104 (22)	12 (2)	0.8 (1.1)
Rubiaceae	*Guettarda elliptica* Sw.	RNG	9	10	14	169 (37)	12 (3)	2.5 (2.3)
Fabaceae-Mimosoideae	*Leucaena leucocephala* (Lam.) de Wit	RNG*	9	12	12	100 (33)	8 (2)	1.8 (1.9)
Fabaceae-Faboideae	*Pictetia aculeata* (Vahl) Urban	RNG	6	13	6	87 (27)	10 (2)	2.7 (2.9)
Nyctaginaceae	*Pisonia albida* (Heimerl) Britton, ex Standl.	RNG	8	9	12	146 (27)	18 (3)	0.0 (0.2)
Nyctaginaceae	*Pisonia subcordata* SW.	RNC	9	12	12	42 (7)	9 (2)	0.0 (0.0)
Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	Private Nursery (Yauco)	9	10	14	99 (19)	16 (3)	0.8 (1.5)

FC - Fideicomiso de Conservación
FWL - U.S. Fish and Wildlife Service nursery in the Cabo Rojo Wildlife Refuge
RNC - Puerto Rico Department of Natural Resources nursery in Cambalache Forest Reserve
RNG - Puerto Rico Department of Natural Resources nursery in Guánica Forest
* Growing voluntarily in pots of other saplings, repotted

Table 4.2. Fire characteristics of burns in Guánica Forest in February 2008. Standard errors are in parentheses. Values that share letters do not vary significantly within columns.

								Mean peak temperature (°C)		
Burn Site	**Fire date and time of day**	**Air Temp. (°C)**	**Relative humidity (%)**	**Avg. Wind Speed ($m \cdot s^{-1}$)**	**Burn area (m^2)**	**Pre-fire biomass ($g \cdot m^{-2}$)**	**Percent biomass consumed**	**Ground level**	**50-cm height**	**100-cm height**
Site 1	Feb. 22, 700 h	22.2	71	0.0	200	616 (72) a	90 (4) a	376 (22) ab	192 (17) a	145 (16) a
Site 2	Feb. 20, 1500 h	25.0	72	3.6	5000	.	.	.	.	.
Site 3 uncut-grass	Feb, 22, 1200 h	28.9	46	4.0	500	476 (95) a	90 (2) a	409 (19) a	155 (15) a	132 (15) a
Site 3 cut-grass	Feb. 22, 1200 h	28.9	46	4.0	300	.	.	289 (22) b	80 (16) b	69 (21) a

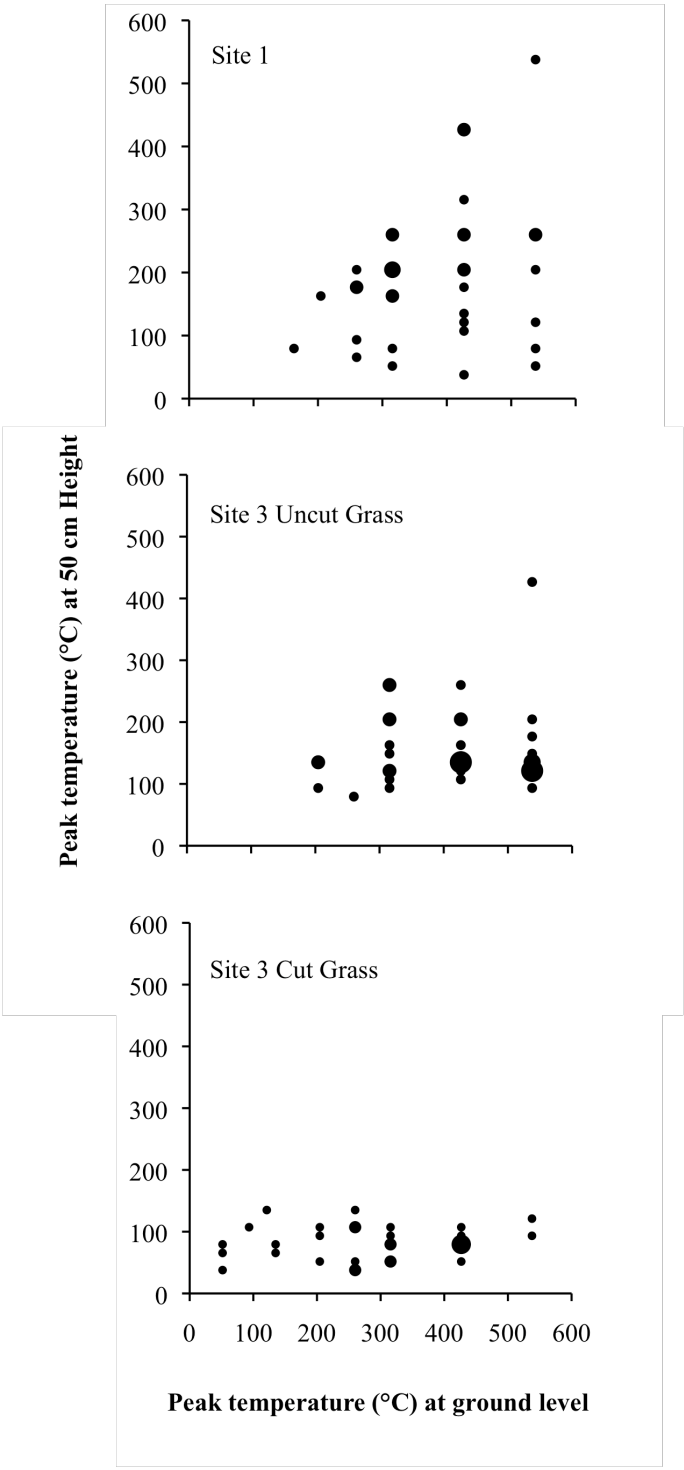

Figure 4.1. Peak temperatures reached during prescribed fires measured with pyrometric paints and chalks. Paired ground-level and 50-cm height measurements were taken on 105 planted saplings. Circle size indicates the number of overlapping points (n = 1 to 5).

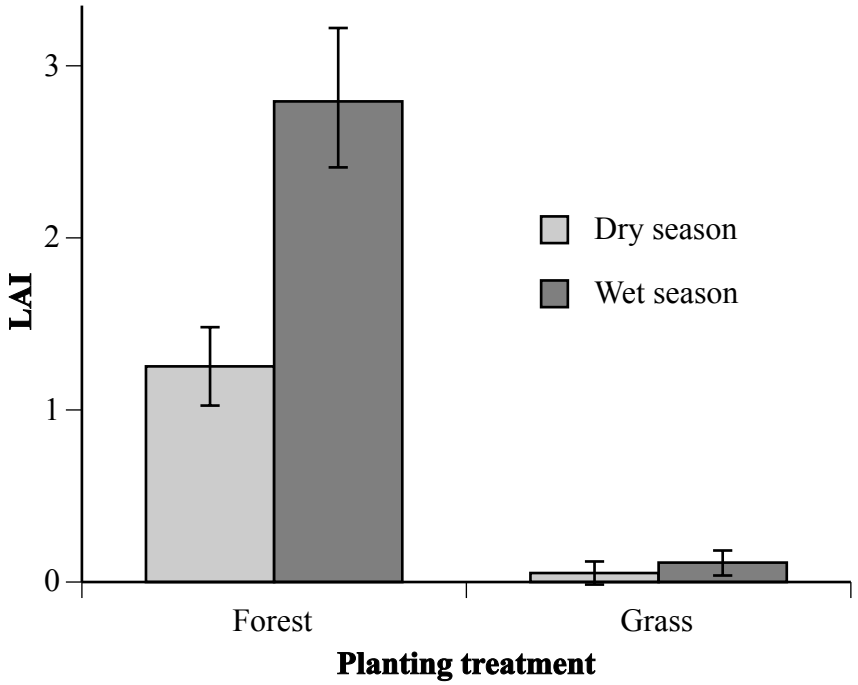

Figure 4.2. Mean LAI at 1-m height in the forest and grass (including burned and unburned) planting plots in the dry (April 2008) and wet (November 2008) seasons. Error bars indicate 95% confidence intervals. All means were significantly different.

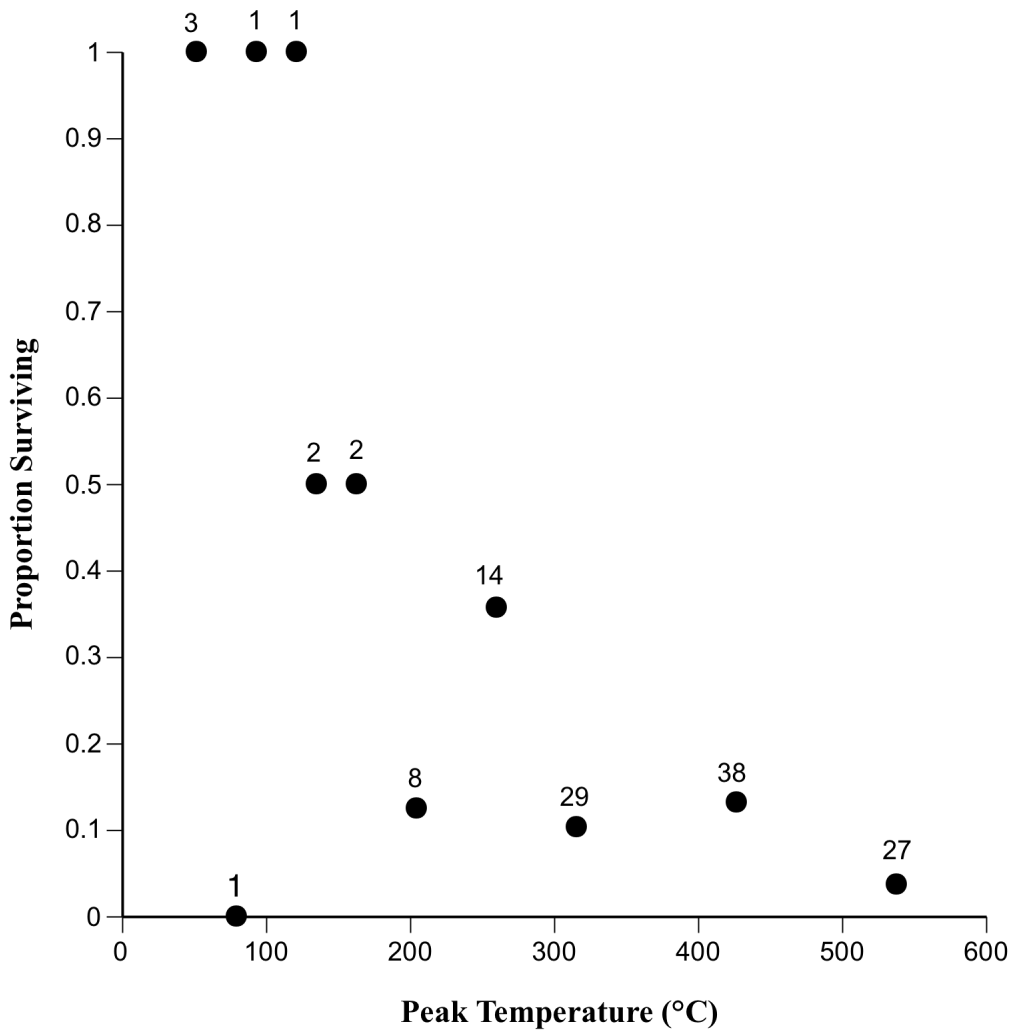

Figure 4.3. The proportion of planted saplings that survived burning in prescribed fires decreased with increasing peak fire temperature at ground height adjacent to their base. The number of saplings measured is indicated above each point.

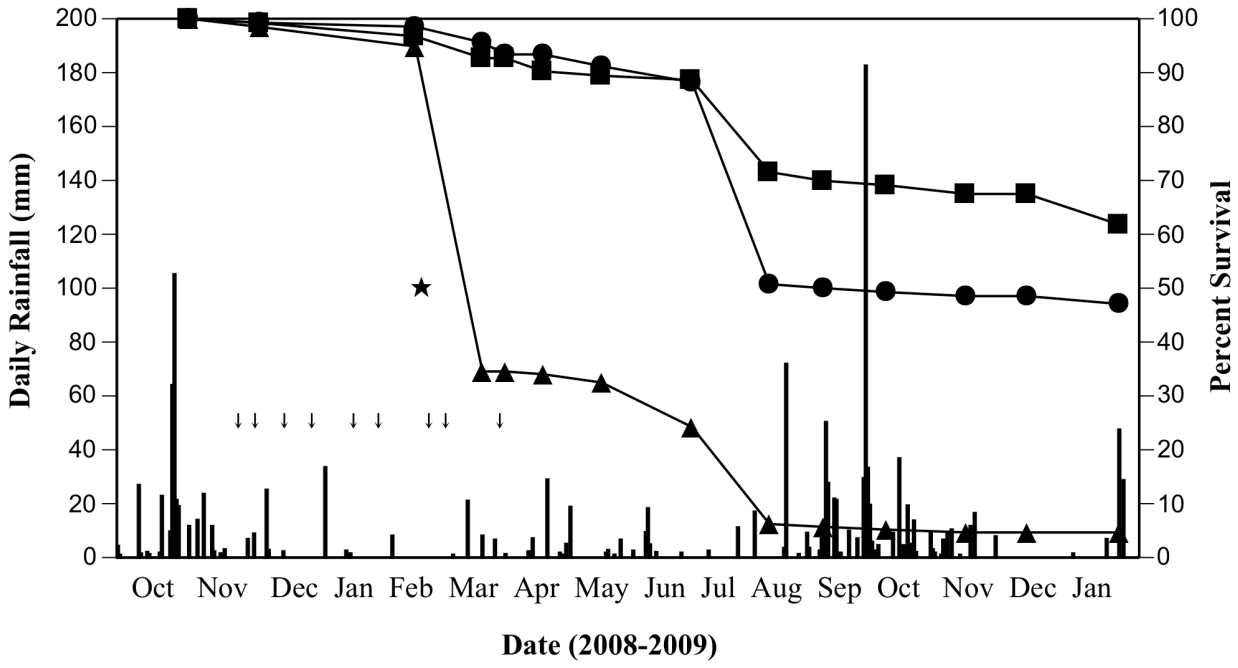

Figure 4.4. Daily rainfall from October 2007 to January 2009 (bars) and percent survival of planted saplings in the three treatments. Squares are the forest treatment. Circles are the unburned grass treatment. Triangles are the burned grass treatment. The star indicates the day of the prescribed fires. Arrows indicate days of supplemental watering.

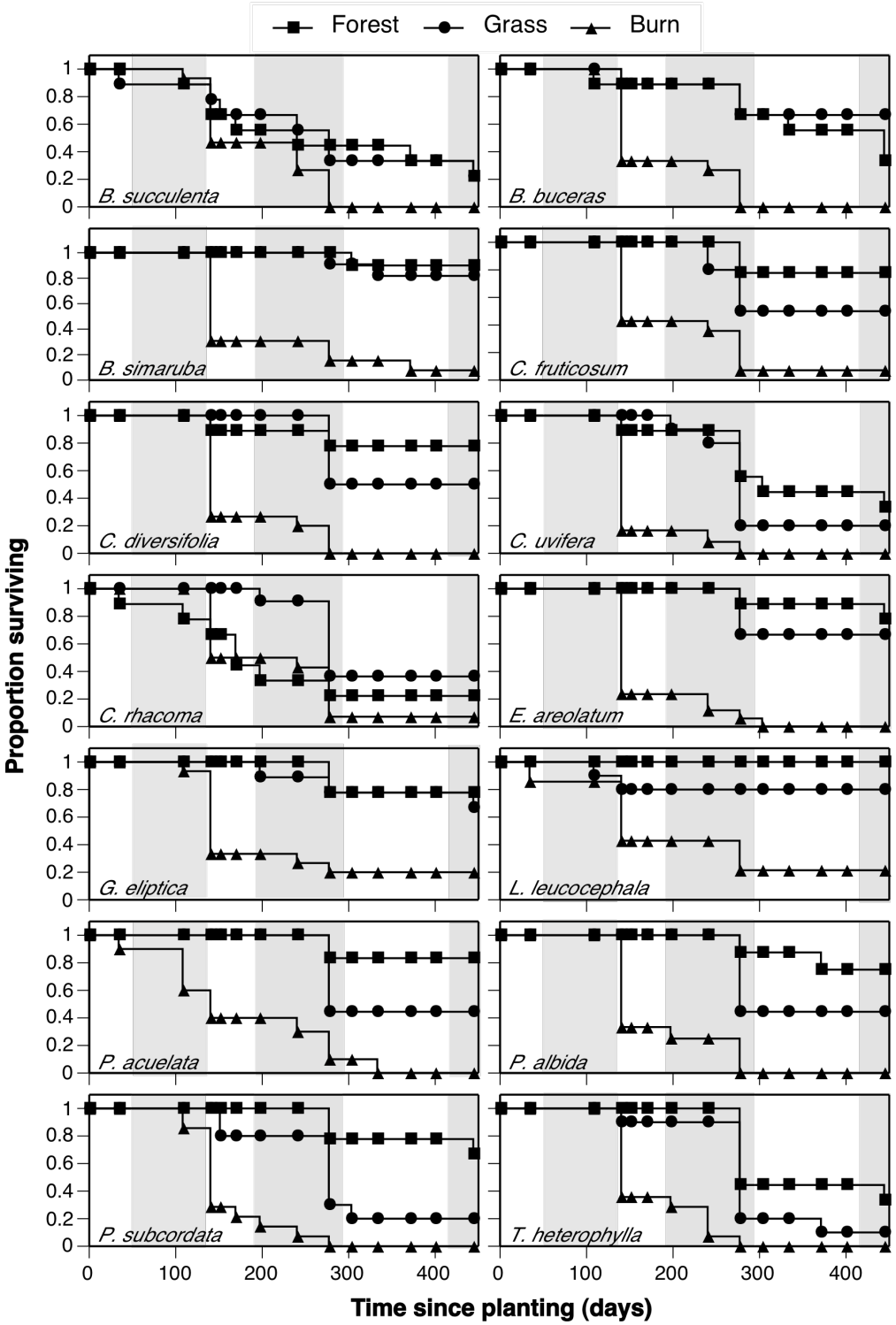

Figure 4.5. Survival of planted saplings (Nov. 4, 2007 – Jan. 21, 2009). Symbols represent census counts. Shaded areas represent dry seasons. Prescribed fires were applied at 110 days.

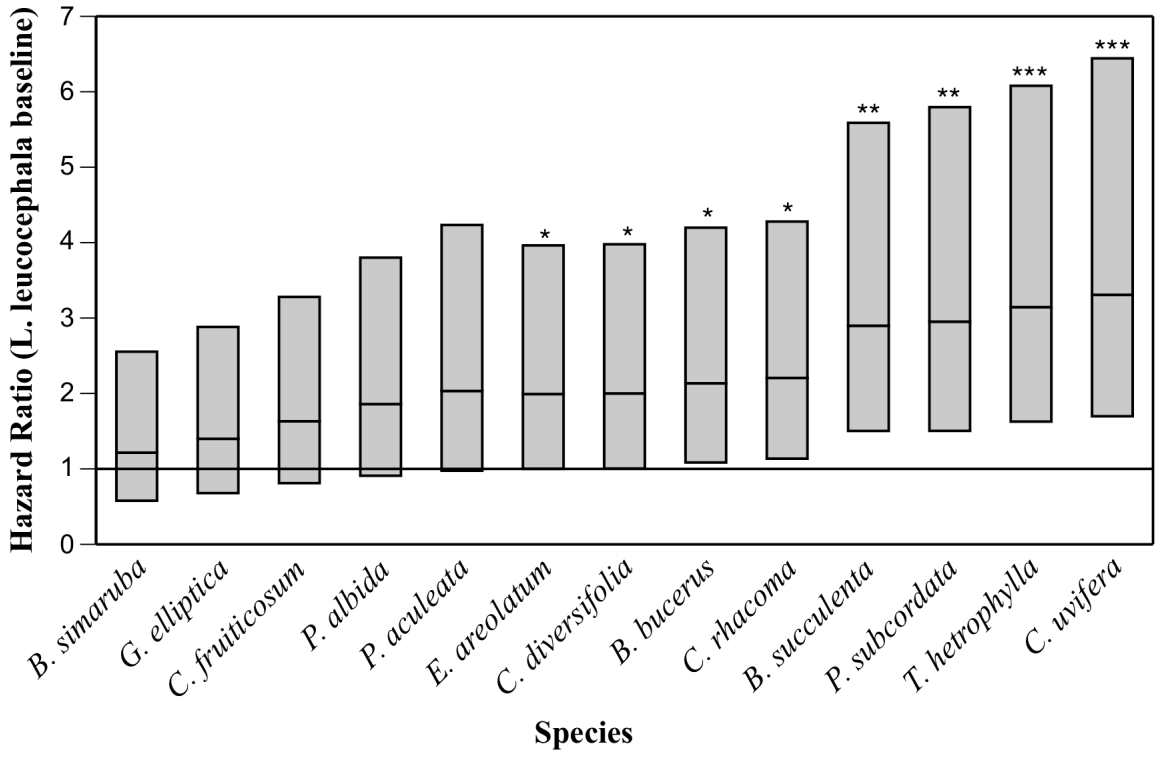

Figure 4.6. Cox proportional hazard ratios for the 13 native tree species compared to *L. leucocephala* in all planting treatments combined. Grey bars indicate the 95% confidence interval of the hazard ratio, which is the line dividing each bar. The hazard ratio indicates the relative probability of mortality during the study period. Values significantly >1 indicate increased probability of mortality compared to *L. leucocephala* and are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

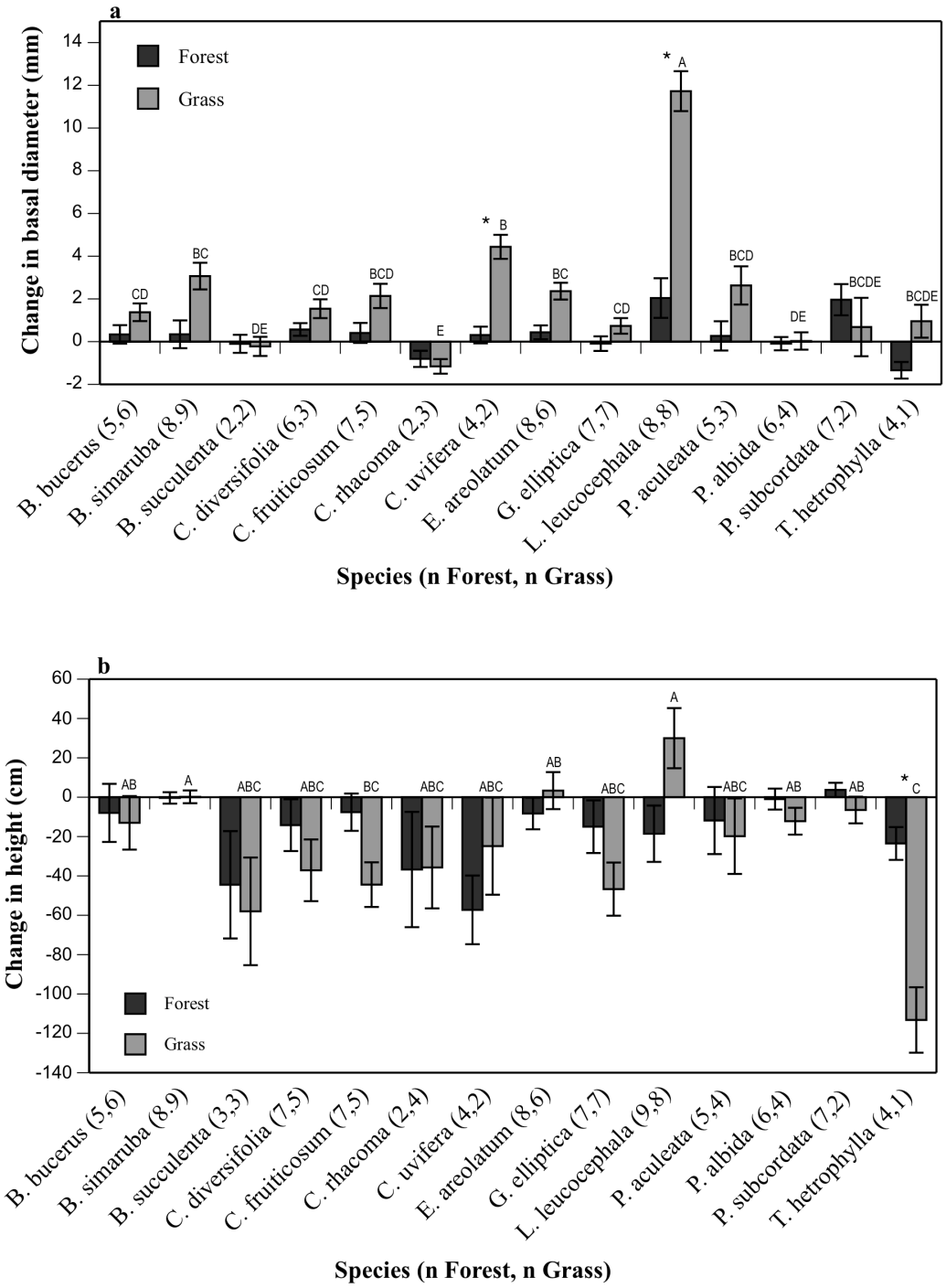

Figure 4.7. Least-square means of change in basal diameter (a) and height (b) of surviving saplings one year after planting. Numbers in parentheses after species names are sample size in forest and grass plots, respectively. Error bars indicate SE. Species that share letters above bars were not significantly different in the grass treatment. Species with an asterisk above bars were significantly different between treatments. In the forest treatment *C. diversifolia* and *P. subcordata* had significantly greater change in basal diameter than *T. heterophylla* and no differences were found among species in change in height.

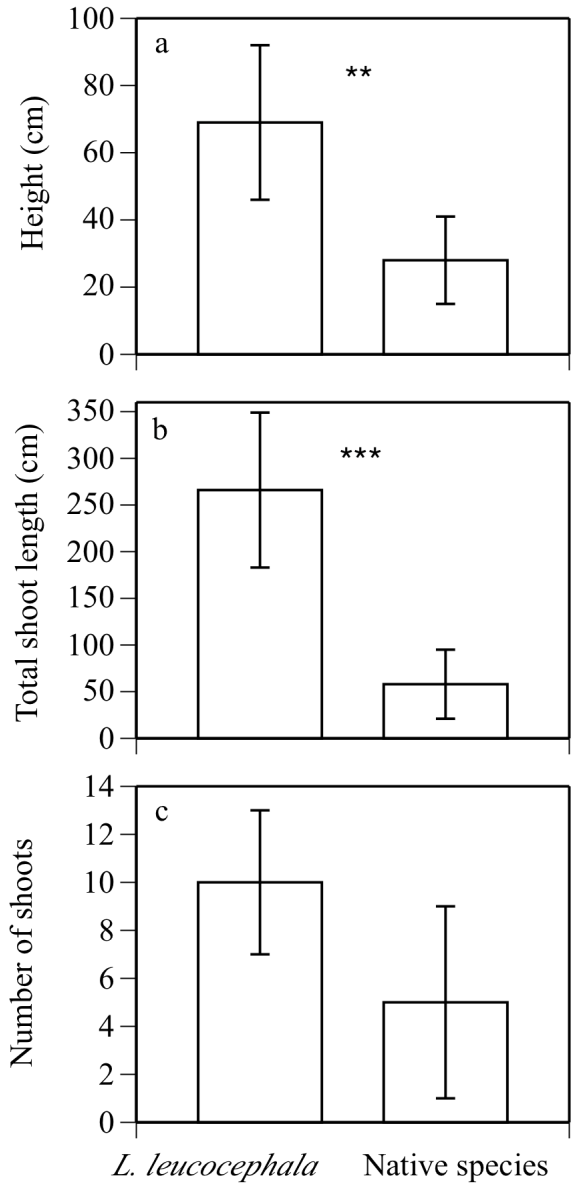

Figure 4.8. Performance of burned saplings eight months after the prescribed fires. Mean (a) height, (b) total shoot length, (c) number of shoots were calculated for the three surviving *L. leucocephala* and six surviving saplings of native species, and then compared with Student's t-tests. ** indicates $p < 0.01$, *** indicates $p < 0.001$.

Chapter 5
Conclusions

Integrating the results from the previous chapters improves the understanding of successional processes that lead to distinct plant communities where fires have occurred in the dry zone of Puerto Rico. These areas are generally invaded by exotic grasses and subject to repeated fires that prevent forest regeneration or they are eventually dominated by the exotic legume tree *L. leucocephala* with native trees of minor importance that increases with time (Weaver and Chinea 2003, Ramjohn 2004, Francis and Parrotta 2006, Molina Colón and Lugo 2006, Pérez Martínez 2007, Weaver and Schwagerl 2008). Fires predominate in forest areas that have already been degraded by agriculture and cutting, but they often encroach on intact forest, further threatening an already scarce habitat. Left unchecked, this progression could slowly erode the remaining patches of dry forest in Puerto Rico and the rest of the Caribbean. An understanding of the ecological processes of post-fire forest regeneration is vital to management plans that are capable of protecting forests from fires and restoring areas that have burned.

I assessed the fire resistance of common dry forest trees, the seed rain in degraded areas, and sapling performance in repeatedly burned areas. This broad focus, spanning whole life stages of trees (seeds, saplings, adults) is a reflection of the current state of knowledge, which has not distinguished the stage that is most influential in determining post-fire plant communities. My thesis has shown that fires have unique effects on plant communities at each of these stages. Below are the most important findings presented in this thesis, their implications for management, and recommendations for future research.

The vast majority of trees in Guánica Forest are susceptible to top-kill from low-intensity fires because they lack the thick bark needed to insulate against flame radiation. The structural physiognomy of the forest – dominated by small-diameter, multi-stemmed trees (Lugo et al. 1978) – compounds this deficiency. Bark thickness of 20 out of the 25 most common tree species could be adequately described with simple linear regressions on stem diameter, but only 16 species reached stem sizes with bark of fire-resistant thickness. Only two species (*B. buceras* and *B. simaruba*) reached this point with stem diameters that were less than 50% of their maximum size and only *B. simaruba* reached bark thickness that would protect against high-intensity fires. These two species are highly over-represented in the scrub forest compared to the deciduous

forest and have been described as trees common in annually burned cattle pastures (Gleason and Cook 1927, Ewel and Whitmore 1973), leading to the speculation that the scrub forest has experienced widespread fires in the past, perhaps in association with goat grazing that occurred in the area until it was designated as protected.

Patterns of seed rain in degraded areas of the dry forest zone of Puerto Rico are greatly influenced by the presence or absence of overstory trees. In open grass areas, the tree seed rain is very low, especially that of animal-dispersed seeds. Although these areas generally become dominated by *L. leucocephala* in the absence of repeated fires, seed rain appears to play a minor role in this pattern – native tree seeds, especially those of wind- and ballistically-dispersed species arrive to these areas at similar – albeit low – rates as *L. leucocephala*. Apparently, subsequent factors such as seed viability, longevity, predation, and germination as well as seedling tolerance of degraded soils, grass competition, and increased solar radiation may favor *L. leucocephala* recruitment in these areas. In areas where *L. leucocephala* dominates the forest canopy, seed rain of native tree species with animal-dispersed seeds increased compared to open grass areas. Utilization of these exotic forest areas by birds and bats could explain this increase in seed input, while the seed rain of abiotically-dispersed native tree species is unaffected by *L. leucocephala.* In this way *L. leucocephala* may act as a facilitator of native forest regeneration in burned and otherwise degraded areas.

The performance of planted saplings in repeatedly burned, grass-dominated areas elucidates the tendency for *L. leucocephala* to eventually dominate them. Nearly all species had increased sapling mortality in grass areas compared to forest understories during a seasonal drought. However, *L. leucocephala* outperformed the native species in the grass areas in terms of growth. It averaged 11.7 mm diameter growth and 30.0 cm height growth in the first year while native species averaged -1.2 to 4.4 mm diameter growth and -113.2 to 3.3 cm height growth. This pattern extended to saplings that were burned in prescribed fires. Although survival in the fires did not differ among species, the surviving *L. leucocephala* resprouted much more vigorously than the surviving native species. However, in forest understories *L. leucocephala* growth was suppressed and it performed similar to native species. These results could be explained by the functional niche of *L. leucocephala* in its native range, where it is a pioneer species that dominates after fires (Allen et al. 1993).

Taken together, these results offer new insights for the formation of management plans that attempt to protect dry forests. Clearly, fire is a disturbance to which native trees are not resistant and it should be prevented and suppressed in areas where forest cover with native species is desired. Grasses form the fuel base for recurrent fires and their removal greatly reduces the likelihood of repeated burning (D'Antonio and Vitousek 1992). Grass suppression through overstory shading is an effective way to reduce fuel loads, but requires that trees are able to grow to form a closed canopy. The slow growth and high mortality rates of native species in grass dominated areas renders them impractical for this purpose. *L. leucocephala*, on the other hand, grew rapidly in grass-dominated areas and showed potential to suppress grasses within a few years. These results support the conclusions of other studies that have recommended *L. leucocephala* for reforestation in degraded Caribbean dry forests (Murphy 1916, Ray and Brown 1995, Francis and Parrotta 2006, Santiago-García et al. 2008). Native forest regeneration could then be augmented with underplanting, although native trees, especially animal-dispersed species, appear to arrive as seeds and grow in the understory of *L. leucocephala*-dominated areas. The most economically prudent reforestation effort may be to passively encourage tree growth (which will generally be *L. leucocephala*) in grass-dominated areas by trimming the grass in places where fires are likely to be ignited (i.e., roadsides) and allowing natural succession to otherwise proceed.

The efficacy of such efforts could be assessed by tracking plant community dynamics in recently burned areas under various management regimes. Space-for-time substitution studies that chronosequence fire effects on plant communities are complicated by the varying long-term land-use histories and uncertain pre-1970's fire histories in much of Guánica Forest and the surrounding area. There are many other important questions that relate to post-fire forest regeneration that have not been addressed. Post-dispersal seed predation has not been studied. Post-fire sprouting ability and long-term survival should be assessed on adult-sized trees. The apparent difficulty that native trees have in establishing and growing in exotic grass-dominated areas of southwest Puerto Rico is likely attributable to the environmental conditions in these areas (e.g., degraded soils and increased air and soil temperatures), competition with grasses for water and nutrients, and the physiological constraints of the trees. However, the extent to which each of these factors determines forest regeneration remains unclear and in need of further research.

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Appendix A. Generalized Linear Model Tables for analyses used in Chapter 3

Test of effects of seed type and site on seed rain in open grass vegetation

Pearson Chi-Square	36.58
Pearson Chi-Square / DF	1.14

Type III Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Seed type	2	32	0.00	0.9995
Site	3	32	0.00	0.9999
Site*Seed type	6	32	0.36	0.8960
Trap(Site)	16	32	1.64	0.1142

Test of effects of vegetation type and site on animal-dispersed seed rain

Pearson Chi-Square	46.92
Pearson Chi-Square / DF	0.59

Type III Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Vegetation type	4	80	6.84	<.0001
Site	3	80	0.00	1.0000
Site*Vegetation type	12	80	2.77	0.0034

Test of effects of vegetation type and site on abiotically-dispersed tree seed rain

Pearson Chi-Square	89.88
Pearson Chi-Square / DF	1.12

Type III Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
veg	4	80	36.92	<.0001
Site	3	80	8.85	<.0001
Site*veg	12	80	4.99	<.0001

Test of effects of vegetation type and site on animal-dispersed seed rain from tree species outside the vicinity of the trap.

Pearson Chi-Square	53.81
Pearson Chi-Square / DF	0.68

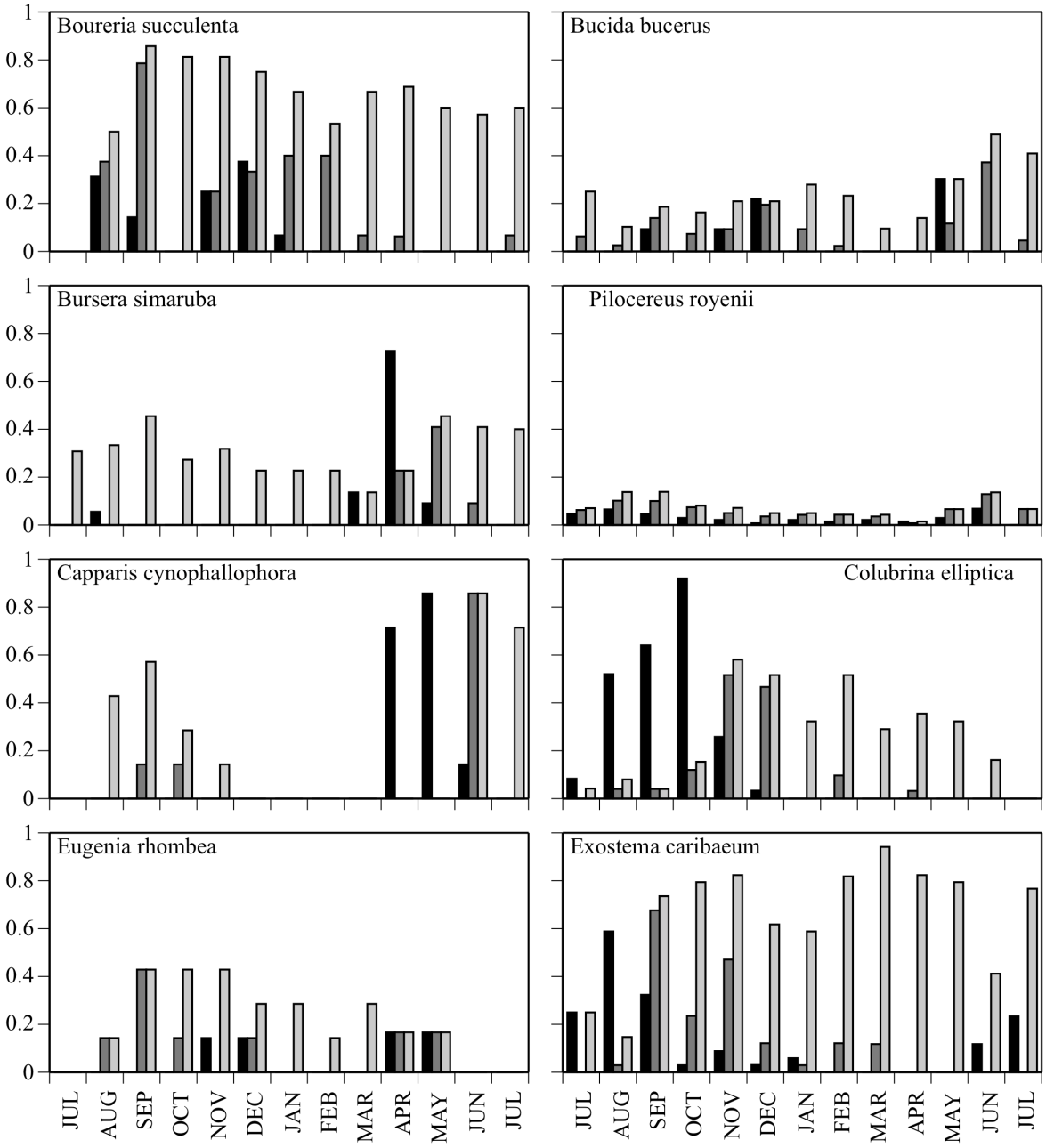
Type III Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
veg	4	79	4.16	0.0042
Site	3	79	0.00	1.0000
Site*veg	12	79	1.20	0.2973

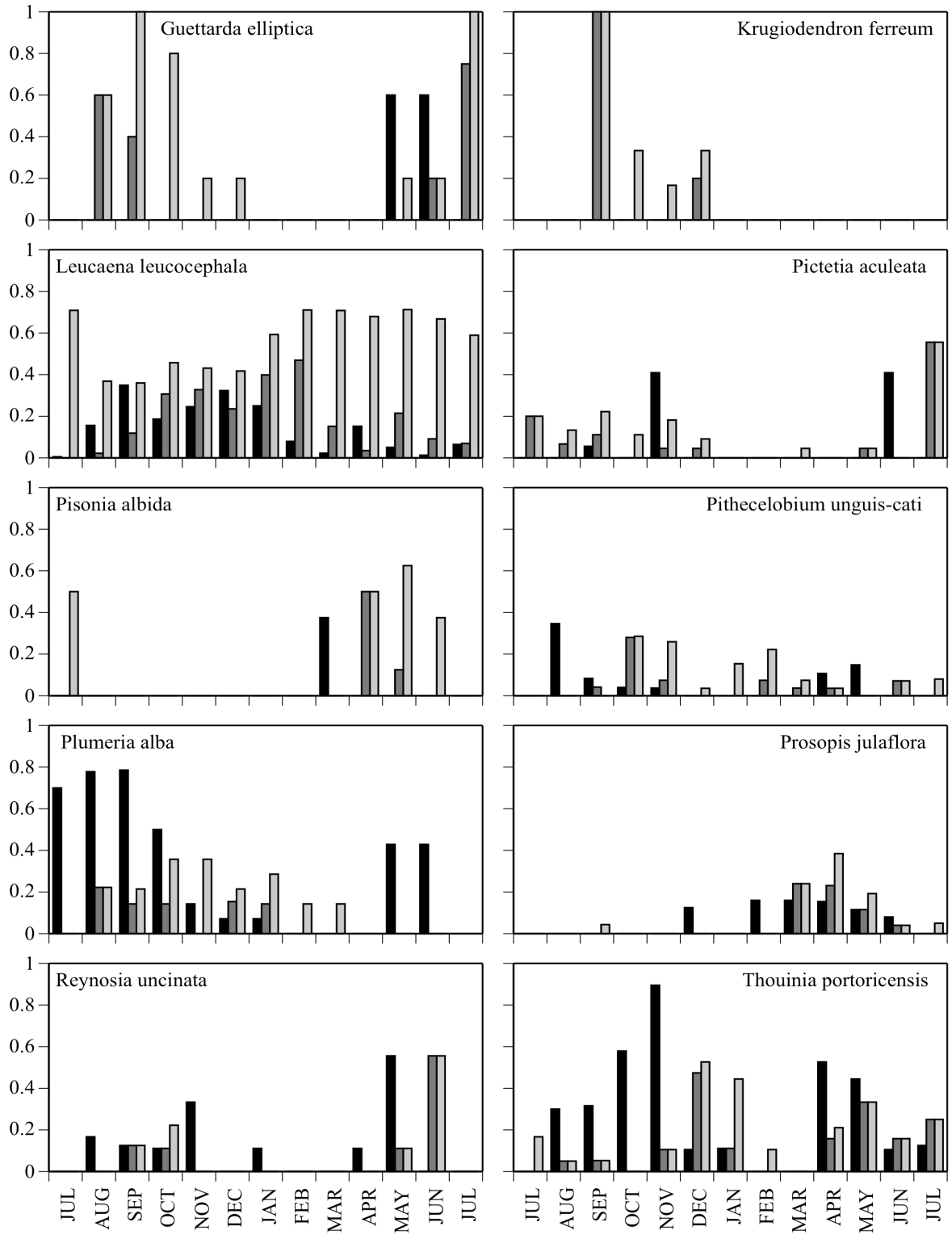
Test of effects of vegetation type and site on abiotically-dispersed seed rain from tree species outside the vicinity of the trap.

Pearson Chi-Square	78.32
Pearson Chi-Square / DF	0.99

Type III Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
veg	4	79	9.97	<.0001
Site	3	79	1.12	0.3446
Site*veg	12	79	2.32	0.0136

Appendix B. Reproductive phenology of common tree species surrounding the seed traps. Only species that had >4 individuals that produced fruit during the 12 mo census are presented. Bars represent the proportion of individuals with flowers (black bars), immature or freshly mature fruit (dark grey bars), and mature or dry fruit (light grey bars).




Guettarda elliptica
Krugiodendron ferreum
Leucaena leucocephala
Pictetia aculeata
Pisonia albida
Pithecelobium unguis-cati
Plumeria alba
Prosopis julaflora
Reynosia uncinata
Thouinia portoricensis
0
0.2
0.4
0.6
0.8
1
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL

Appendix C: ANOVA Tables for statistical tests performed Chapter 4. Num DF is numerator degrees of freedom. Den DF is denominator degrees of freedom.

ANOVA Table for peak fire temperatures

Effect	Num DF	Den DF	F Value	Pr > F
treatment	2	8	11.08	0.0049
height	2	131	221.71	<.0001
treatment*height	4	131	2.32	0.0607

ANOVA table for LAI

Effect	Num DF	Den DF	F Value	Pr > F
site	2	29	1.80	0.1833
treatment	1	29	1110.35	<.0001
season	1	30	633.63	<.0001
treatment*season	1	30	411.55	<.0001

ANOVA table for change in basal diameter

Effect	Num DF	Den DF	F Value	Pr > F
species	13	95	16.55	<.0001
treatment	1	15	38.80	<.0001
species*treatment	13	95	7.36	<.0001
site	2	15	0.34	0.7171

ANOVA table for change in height

Effect	Num DF	Den DF	F Value	Pr > F
species	13	103	7.40	<.0001
treatment	1	15	2.16	0.1624
species*treatment	13	103	3.36	0.0003
site	2	15	4.25	0.0346